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ОБЗОРНЫЕ СТАТЬИ

GAMETE STRUCTURE AND DEVELOPMENT IN CONNECTION WITH FERTILIZATION IN ANGIOSPERMS

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The paper analyzes data on the processes occurring before and during fertilization in flowering plants. At the gametophyte stage, the gametes are formed from haploid microspores and megaspores. They are sperms, egg and central cell. The fusion of male and female gametes occurs after the pollen tube enters any synergid. One sperm fuses with the egg cell, and another from the same pollen tube joins with the central cell.

The angiosperms are likely to have four types of fertilization. These types differ in the degree of completion of syngamy. Premitotic and postmitotic types are characterized by complete syngamy, and androgamic and gynandrogamic types are inherent in incomplete syngamy. In this case, the behavior of the sperm nuclei is of great significance. They, as a rule, combine with the nuclei of female gametes (premitotic and postmitotic types), but the sperm nuclei can remain independent (gynandrogamic type) or a female nucleus is replaced by a male one (androgamic type). The premitotic type of fertilization follows the way in which the gamete protoplasts and nuclei are united before the mitosis in the zygote nucleus. As for the postmitotic type, it is carried out on a completely different basis. It is possible that in angiosperms the chromosomes of sperm and egg cell do not unite during mitosis. They further divide independently, and a diploid set of chromosomes arises in a 2-celled embryo.

Keywords: male and female gametes, fertilization, syngamy, triple fusion, fertilization types, angiosperms

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The gametes, represented in angiosperms by sperms and egg cells, unlike somatic cells, have a haploid set of chromosomes. The places of localization, the time of the appearance of gametes during ontogenesis, the features of differentiation and transformation, as well as some other structural characteristics are specific. Of considerable scientific interest is the hypothesis of the similarity of fertilization processes in plants and animals. According to this hypothesis, in plants, like animals, there are two types of fertilization, depending on when the nuclei of sexual cells unite: premitotic (before mitosis of the zygote nucleus) and postmitotic (after the onset or during division of the zygote) (Gerassimova-Navashina, 1947, 1957, 1960, 1969, 1990). Available information in the literature indicates that general principles of fertilization mechanisms in animals and flowering plants are more conserved than previously thought. Among them there are following aspects: structure of gametes, cell–cell communication events between gametes as well as their physical interaction and fusion during fertilization (Marton, Dresselhaus, 2008; Dresselhaus et al., 2016; Shin et al., 2021). However, the types of fertilization were not considered.

Fertilization of the central cell by sperm has been studied in a small number of flowering plants, and this process is given less attention than the study

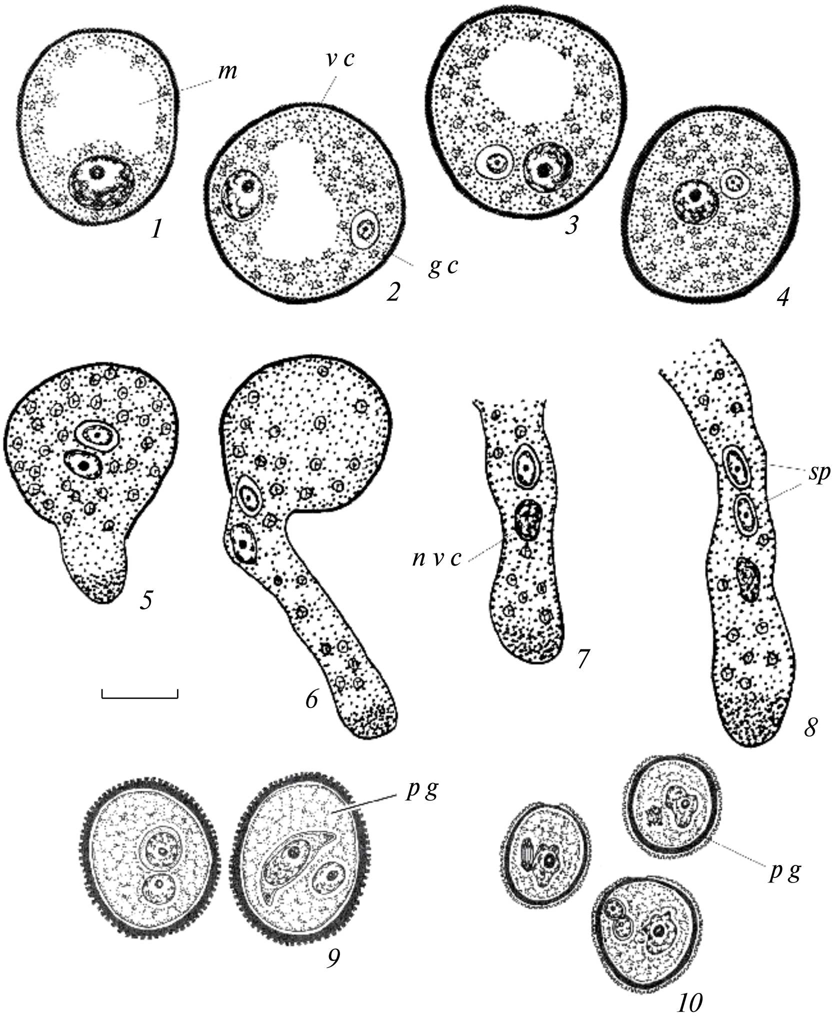

Fig. 1. Formation of pollen grains and pollen tubes. *1–4* – *Ceratophyllum demersum*, *5–8* – *C. platyacanthum* (Ceratophyllaceae), *9* – *Gagea stipitata* (Liliaceae), *10* – *Hemerocallis citrina* (Hemerocallidaceae). (*1–8* – after Shamrov, 1983; *9* – after Shamrov, 1990a; *10* – after Shamrov, 1990b). *g c* – generative cell, *m* – microspore, *n v c* – nucleus of vegetative cell, *p g* – pollen grain, *sp* – sperm, *v c* – vegetative cell. Scale bar, µm: 30.

of the egg (syngamy). Since in flowering plants the endosperm resulting from triple fusion is necessary for coordinating the development of the embryo and seed germination, its formation usually begins before the division of the zygote. That is why the way of endosperm formation does not always correspond to the type of fusion of female and male gametes during syngamy and most often occurs according to the premitotic type or is characterized by signs of premitotic and postmitotic types. Thus, for *Triticum aestivum* L. and *Zea mays* L. (Poaceae), it was shown that, although double fertilization occurs according to the premitotic type, the sperm chromosomes of the resulting nucleus of the primary endosperm cell enter prophase separately from the chromosomes of the polar nuclei. Complete union of sperm chromatin and polar nuclei occurs in metaphase, as in the postmitotic type (Batygina, 1974; Korobova, 1982). In *Zephyranthes candida* Lindl., *Z. grandiflora* Lindl. and *Z. macrosiphon* Baker (Amaryllidaceae), syngamy occurs according to the premitotic type; in the first two species the fusion of the central cell and sperm is also premitotic, while in *Z. macrosiphon* it is postmitotic (Vorsobina, Solntseva, 1979). In *Dioscorea caucasica* Lipsky (Dioscoreaceae) the triple fusion is similar to the syngamy of the premitotic type. In another species, *D. nipponica* Makino, an intermediate nature of the fusion of sperm and central cell was revealed (Torshilova, 2018).

For a number of flowering plants, it was shown that the process of syngamy is simultaneously characterized by traits of different types. An electron microscopic study revealed that the fusion of the sexual nuclei is carried out according to a united plan, while they actually represent a single lobed nucleus, and the patterns of different types of fertilization at the light-optical level represent differences in the rate of their complete union (Plyushch, 1992).

A comparative analysis of syngamy in plants and animals revealed that in the postmitotic type in plants, sperm enters the egg, while in many animals, the spermatozoid penetrates into developing oocyte during the first or second division of meiosis and activates it for further development (Shamrov, 2015b). It was the presence of a number of contradictions in the literature that prompted us to analyze the available data not only on syngamy, but also on the features of the formation of sexual cells that are involved in its passage.

Gametogenesis. In flowering plants, male gametogenesis is a long process and occurs within specialized gametophytes that develop in anthers. The male gametophyte is represented by pollen grains, 2-celled (Fig. 1, *1–4, 9*) or 3-celled (Fig. 1, *10*). In 2-celled pollen grains, gametes are not yet formed, and they arise during the growth of the pollen tube (Fig. 1, *5–8*). In both variants, the gametes are sperm-cells (Shamrov, 2015a).

Sperms are connected to each other by a common median cell plate or by protrusions of their protoplasts using structures resembling plasmodesmata (Russel, Cass, 1981). Detailed studies on sperm formation have been carried out. In *Hordeum* species (Poaceae), during the division of the generative cell, organelles move to the peripheral regions of the cytoplasm. Microtubules, individual cisterns of the granular endoplasmic reticulum, and many free ribosomes are found in the area of the spindle. In the late telophase, vesicles of dictyosomes and microtubules are located in the center of the phragmoplast, where the median cell plate is formed between the sperms (Charzynska et al., 1988). In *Nicotiana tabacum* L. (Solanaceae), the division of the generative cell is also accompanied by the formation of a phragmoplast between the protoplasts of two sperms (Palevitz, 1993), while in *Tradescantia virginiana* L. (Commelinaceae), this process occurs without the participation of the phragmoplast and is characterized by the formation of a constriction (Palevitz, Cresti, 1989). In flowering plants, one sperm cell has a cytoplasmic projection with the nucleus of a vegetative cell. The *Male Germ Unit* (MGU) appears and moves towards the embryo sac (Dumas et al., 1985). The cytoplasmic projection plays a structural role in linking the male germ unit, but potentially can perform other important roles (McCue et al., 2011). There is an opinion that such a complex arises already in a 2-celled pollen grain, while the nucleus of the vegetative cell contacts the cytoplasmic "tail" of the generative cell (a large number of microtubules are located here) (Ermakov et al., 2016).

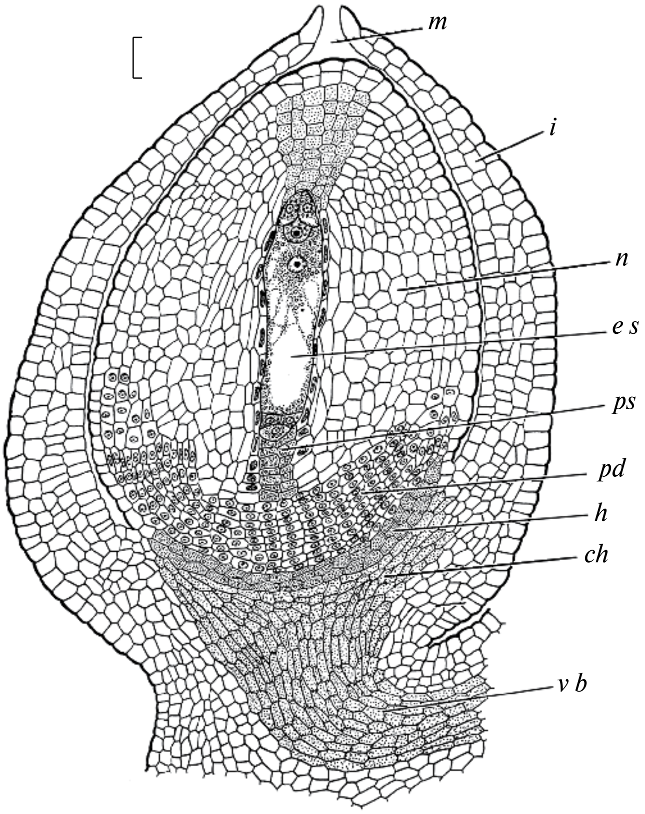

Fig. 2. Mature ovule structure in *Ceratophyllum demersum* (Ceratophyllaceae) (after Shamrov, 1997). *e s* – embryo sac, *h* – hypostase, *i* – integument, *m* – micropyle, *n* – nucellus, *pd* – podium, *ps* – postament, *v b* – vascular bundle. Scale bar, μm: 30.

In most flowering plants, the sperms are isomorphic, but in some, their dimorphism is noted – the sperms of one pair differ in size, amount of cytoplasm, and volume of nuclei. In *Plumbago zeylanica* L. (Plumbaginaceae), the larger sperm is in contact with the nucleus of the vegetative cell (Russell, 1984). In *Nicotiana tabacum*, the sperm that is not associated with the nucleus of a vegetative cell is smaller, richer in plastids, and poor in mitochondria compared to the associated sperm (Yu et al., 1992). Dimorphism was found in members of other families of flowering plants:

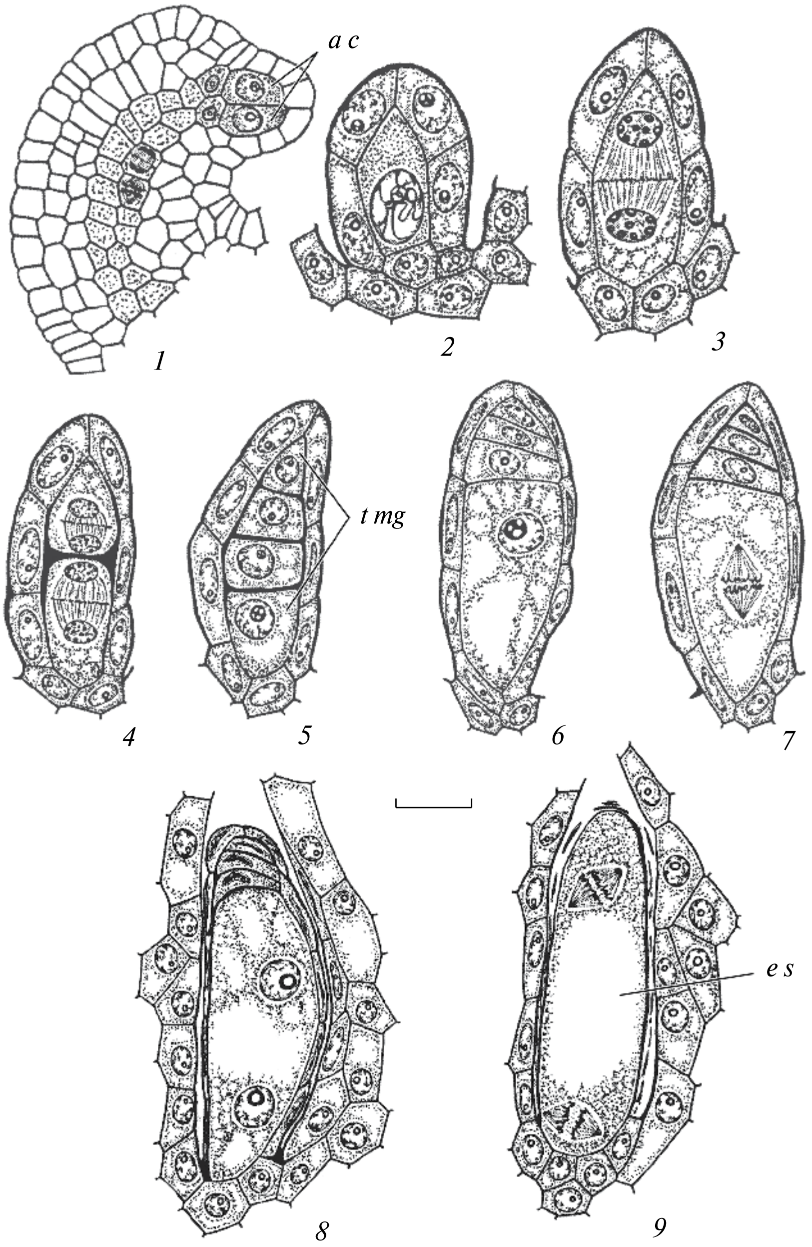

Fig. 3. Ovule structure at archesporium stage (*1*), megasporogenesis (*2–5*) and first stages of embryo sac development in (*6–9*) in *Gentiana lutea* (Gentianaceae) (after Shamrov, 1988). *1–9* – stages of development. *a c* – archesporial cells, *e s* – embryo sac, *t mg* – tetrad of megaspores. Scale bar, μm: 30.

Chenopodiaceae – *Spinacia oleracea* L. (Wilms, 1986), Brassicaceae – *Brassica campestris* L. and *B. oleracea* L. (Dumas et al., 1985), Poaceae – *Zea mays* (Rusche, Mogensen, 1988), Euphorbiaceae – *Euphorbia dulcis* L. (Murgai, Wilms, 1988), Ericaceae – *Rhododendron macgregoriae* F. Muell. (Taylor et al., 1989), Liliaceae – *Gagea lutea* (L.) Ker Gawl. (Yang et al., 1995). The contractile proteins (myosin and actin), which are part of microfilaments, were found in the cytoplasm of a vegetative cell. Myosin is located on the nucleus of a vegetative cell and is associated with male gametes using short actin microfilaments (Heslop-Harrisson J., Heslop-Harrisson Y., 1989; Russell, 1992; Knox et al., 1993).

Female gametophytes are represented by embryo sacs of different structures, depending on the type of their development. Their formation occurs in the ovule (Johri, 1963; Shamrov, 2008; Rudall, 2021). The ovule of angiosperms is an organ comprising the nucellus, integuments, chalaza, and funiculus. The events of archesporium differentiation, megasporogenesis and embryo sac formation take place in it (Fig. 2). After fertilization both the embryo and endosperm arise. The complex transformations of the embryo, endosperm and surrounding tissues developing in conjunction with them result in the seed formation. The ovules and seeds are characterized by considerable diversity in the shape, the degree of development and the structure (Shamrov, 2018). Various specific structures are formed in the nucellus, that provide differentiation. The postament is a column-like tissue located below the sporogenous or gametophytic structures. The podium is a cup-shaped structure arising in the chalazal zone of the nucellus. The hypostase is a boundary tissue between the nucellus, integuments and chalaza. The major function of all the special structures in question appears to be that of directed translocation of nutrients: the hypostase – to the nucellus and integuments; the podium – to the lateral (lateral transport through integumentary tapetum and central cell) and, presumably, apical nucellar regions (apical transport through synergids and parietal tissue); and the postament – to the basal nucellar region (basal transport through antipodals) (Shamrov, 2008, 2022).

Female gametophyte in angiosperms consists of egg apparatus, antipodals, and central cell. The egg apparatus is presented by egg and two synergids (*Female Germ Unit* – FGU). This notion was proposed by Dumas et al. (1984). Subsequently, the content of this concept was expanded. Now the female germ unit is comprised of the egg, two synergids, and the central cell (Huang, Russell, 1992). The female gametes are the egg and the central cell (Fig. 3, *1–9*; 4, *1–6*). The egg is located on the side, usually slightly below the synergids. It, as a rule, has a pear-shaped shape and is characterized by morphological polarity: the nucleus is located at the apical end, and the vacuole is located at the basal pole. The synergids are egg-like and are also characterized by polarity, with the nucleus at the basal end and the vacuole at the apical pole or center of the cells (Fig. 4, *5, 6*; 5, *1–3*). In the largest central cell of the embryo sac, 2 polar nuclei most often form (Fig. 4, *4*), which usually fuse to form a secondary nucleus before fertilization (Fig. 4, *6*; 5, *1–3*). The antipodal cells are arranged in the form of a triangle or a line of three cells and are localized at the chalazal pole of the embryo sac (Fig. 4, *6*; 5, *1*). They may be ephemeral and disappear before or during fertilization. Remaining after fertilization, the antipodes can increase in size, while they show polyploidization of nuclei (Ceratophyllaceae, Gentianaceae, Ranunculaceae, etc. – Zhukova, Sokolovskaya, 1977; Shamrov, 2008; Butuzova, 2018) (Fig. 5, *2*). In some plants, there is an increase in the number of antipodes (Nelumbonaceae – Titova, 1988), which is accompanied by an increase in the ploidy of nuclei in cells (Poaceae, etc. – Batygina, 1974). Antipodal cells are equipped with complete cell walls. They are organized according to the transfer cells, and play an important role in the nutrition of the embryo sac, performing the functions of adsorption, transport, and synthesis of a number of metabolites.

In the formed embryo sac of many plants, all cells of the egg apparatus have a complete cell walls. In the process of maturation of the embryo sac in the apical parts of the egg and synergids, some of the cell walls are lost (possibly, substances cease to accumulate in them), and before fertilization, the protoplasts of these cells (on the side of the central cell) are surrounded only by the plasmalemma (Russell, 1992). In the basal part of the synergids, a filiform apparatus differentiates – a system of winding, highly branched outgrowths of the cell wall (Fig. 4, *6*; 5, *1*). Such outgrowths increase the surface of the plasmalemma, which gives it the properties of transfer cells for the transport of substances. The central cell in the area of contact with the egg is also covered with a plasmalemma. Here, an extracellular space, or “gap”, is formed, where sperms enter. It is designated as the gamete interaction zone (Sprunck et al., 2012).

Fertilization traits in angiosperms and gymnosperms in the light of endosperm origin. In gymnosperms (Goroschankin, 1880) and angiosperms (Strasburger, 1884; Guignard, 1886), like other higher plants, single fertilization was first described. It was believed that the second sperm of the pollen tube is destroyed and does not participate in fertilization. However, double fertilization was later found in flowering plants, which is one of the distinguishing characteristics of these plants. It includes the union of one sperm with an egg (later, an embryo is formed from the resulting zygote), and the second sperm (of the same pair) with the central cell of the embryo sac (endosperm develops).

The phenomenon of double fertilization was discovered in the study of fertilization in *Fritillaria tenella* M. Bieb. and *Lilium martagon* L. from the Liliaceae family (Nawaschin, 1898a, b). Both

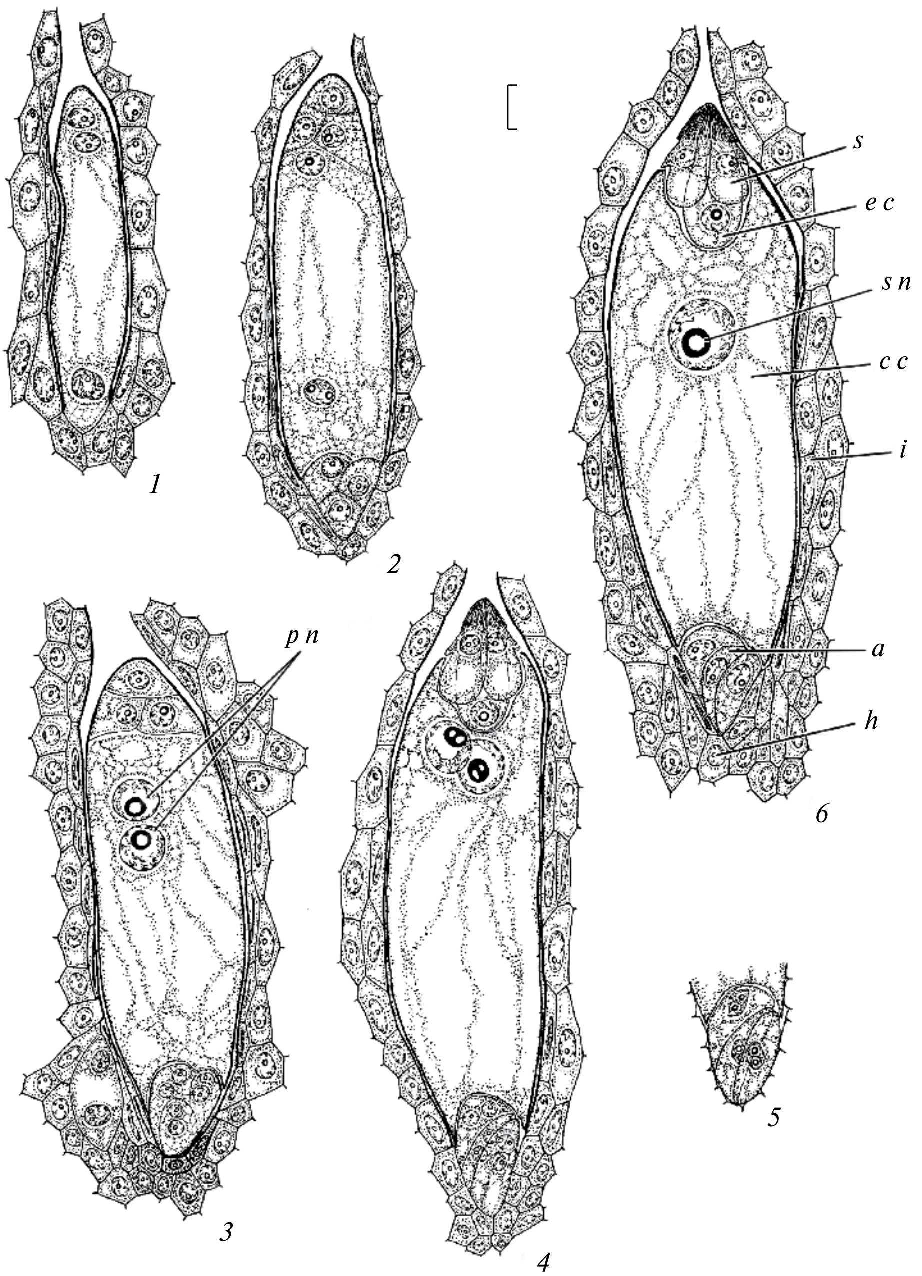

Fig. 4. Final stages of embryo sac formation in *Gentiana lutea* (Gentianaceae). *1–6* – stages of development (after Shamrov, 1988). *a* – antipodal cells, *c c* – central cell, *e c* – egg cell, *h* – hypostase, *i* – integument, *p n* – polar nuclei, *s* – synergid, *s n* – secondary nucleus of central cell. Scale bar, µm: 30.

fertilizations were recognized as real sexual acts and compared with polyembryony. Later, also on the example of lily plants, the concept of double fertilization was confirmed, while the author, Guignard (1899) refers to the results obtained earlier by Nawaschin (1898a, b). But the French researcher not only confirmed the fusion of two male gametes of one pollen tube with the egg and the central cell, but also accompanied the descriptions with illustrations of these processes. By the way, the term "double fertilization" appeared later (Nawaschin, 1900). Unfortunately, there is still a point of view that Nawaschin (1898a, b) and Guignard (1899) discovered independently the phenomenon of double fertilization in flowering plants (Friedman, 1998; Faure, Dumas, 2001).

At the end of the 20th century, it was shown that double fertilization can occur in some gymnosperms from the Gnetales (*Ephedra*, *Gnetum*) (Friedman, 1990, 1991; Carmichael, Friedman 1995). However, the question legitimately arises, are the processes of double fertilization homologous in angiosperms and gymnosperms? A detailed study revealed that in *Ephedra nevadensis* S. Watson and *E. trifurca* (Stapf) V.A. Nikitin, the second sperm fuses with the abdominal (ventral) tubular cell, which is preserved in the archegonial cavity, forming an additional embryo (Friedman, 1990, 1991). This was also noted in other gymnosperms, but the second embryo did not develop. In gymnosperms, the formation of an additional embryo is more similar to the simultaneous formation of two embryos of flowering plants, when not only the egg is fertilized, but also one of the synergids.

Angiosperm synergid can probably be compared to the ventral tubular cell of the gymnosperms, which shares a common genesis with the egg cell, since both originate from the same cell. When an egg and a synergid are fertilized by two sperms from one pollen tube, flowering plants lose the possibility of fertilization of the central cell, and without endosperm the embryo is destroyed (Lakshmanan, Ambegaokar, 1984). In *Arabidopsis thaliana* (L.) Heynh. (Brassicaceae) mutants with impaired auxin biosynthesis, all cells of the embryo sac can develop either along the synergid pathway or the egg cell pathway (Pagnussat et al., 2009), or two egg cells and one synergid are formed in the egg apparatus, and after fertilization in the latter case, 2 embryos are formed, and the endosperm does not appear (Berger, Twell, 2011). In *lis* mutants of *A. thaliana*, accessory cells of female gametophyte (synergids, antipodals) differentiate gametic cell fate, indicating that LIS is involved in a mechanism that prevents accessory cells from adopting gametic cell fate. The temporal and spatial pattern of LIS expression suggests that this mechanism is generated in gametic cells (Groß-Hardt et al., 2007).

It is known that Nawaschin (1898a, b) compared double fertilization with polyembryony. The same point of view is shared by Friedman (1994), who believes that two embryos arise in angiosperms as a result of fertilization, one of which gradually began to function as an endosperm. These ideas were developed by him in subsequent works (Friedman, Williams, 2004). However, simultaneously developing embryos inevitably enter into competition for nutrients, and it is difficult to imagine that one of the embryos "voluntarily" would begin to feed the remaining embryos. If this could happen, then only when one or several embryos ceased to develop further, and the resulting plastic substances were used by the plant for the final formation of a single embryo. Raghavan (2003) assessed the presence of double fertilization in some gymnosperm species. The product of the second fusion in gymnosperms is a transient embryo, rather than the endosperm as in angiosperms.

According to the second hypothesis (Strasburger, 1900; Coulter, 1911) endosperm of flowering plants represents a homolog of a portion of the gymnosperm gametophyte that later became sexualized. The second fertilization event of the central cell by an additional sperm cell might have provided some unknown fitness advantages to the growing embryo. The endosperm would then have originated from mutation the female gametophyte of gymnosperms, which predestine these cells for a supporting nonreproductive role (Linkies et al., 2010). According to Baroux et al. (2002), this theory is supported by the fact that the addition of the paternal genome to the maternal central cell might create hybrid vigor.

It should be emphasized that the endosperms in angiosperms and gymnosperms, while performing a similar function, have a different origin. In gymnosperms, the endosperm is the female gametophyte. One or more peripheral cells in its micropylar part give rise to archegonia. The cells adjacent to the archegonium transform into a sheath. The remaining cells of the female gametophyte during the period of embryo development are transformed into the storage tissue of the seed (Singh, 1978; Trenin, 1988). A similar nutrient tissue, called perisperm, is formed in flowering plants after fertilization due to the accumulation of nutrients in the remaining cells of the megasporangium (nucellus) of the crassinucellate ovule. Perisperm was found in seeds of primitive (Cabombaceae, Cannaceae, Costaceae, Marantaceae, Nymphaeaceae, Zingiberaceae) and some advanced (Amaranthaceae, Caryophyllaceae, Phytolaccaceae, Portulaceae) families (Shamrov, 2008). Unlike the endosperm of gymnosperms and the perisperm of flowering plants, the endosperm of angiosperms, having a sexual nature, performs not only a trophic function (as considered Strasburger, 1900; Coulter, 1911), but also participates in the provision and distribution of signals that regulate the processes of differentiation and organogenesis of the embryo (Chen et al., 2014). These signals include

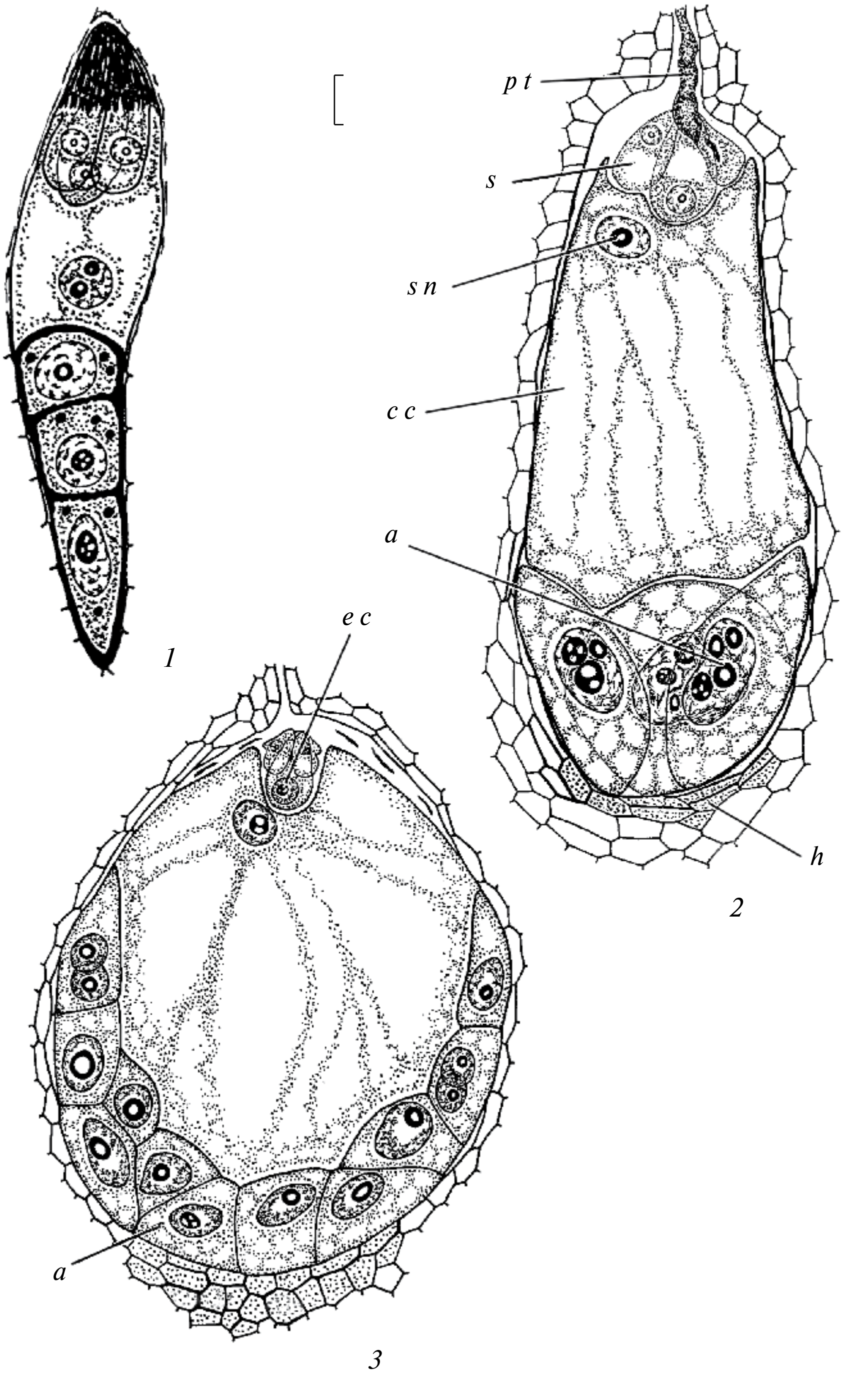

Fig. 5. Mature embryo sac structure in *Hemerocallis hybrida* (Hemerocallidaceae) (*1*), *Gentianopsis barbata* and *Gentianella lingulata* (Gentianaceae) (*2, 3*). (*1* – after Shamrov, 1990b; *2, 3* – after Shamrov, 1988). *a* – antipodal cells, *c c* – central cell, *e c* – egg cell, *h* – hypostase, *p t* – pollen tube, *s* – synergid, *s n* – secondary nucleus of central cell. Scale bar, µm: 30.

dipeptides (Costa et al., 2014) and phytohormones, among which auxin plays a central role (Locascio et al., 2014; Doll et al., 2017).

In the absence of endosperm, the embryo stops developing at the globular stage. Thus, the endosperm in flowering plants is probably a *de novo* structure. In flowering plants, it does not give rise to a new organism. Its cells become specialized very early, and even under *in vitro* culture conditions, it was not possible to convincingly prove the emergence of embryos of endosperm origin (Johri, Ambegaokar, 1984). The significance of the endosperm, which occurs during the fertilization of the central cell by sperm, becomes especially important in plants during apomixis (primarily Poaceae). In this case, the parthenogenetic embryo does not start differentiation and histogenesis on its own and is forced to wait for the moment when, as a result of pseudogamy, the sexual endosperm is formed and starts this process (Yudakova et al., 2018). The significance of the endosperm resulting from the fertilization of the central cell is especially important when considering adventitious embryos. Embryos arise from somatic cells of the nucellus or integument near the embryo sac, but embryogenesis begins only after pollination, when the zygotic embryo stops developing, and apomixis replaces amphimixis in the developing seed as an alternative system. The existing endosperm system of a sexual nature allows nucellar and integumental embryos that have entered the cavity of the embryo sac to complete the normal course of development (Shamrov, 2019).

However, the relationships between the embryo and the endosperm are probably more complex. It was studied the *Arabidopsis thaliana* mutation Cdc2, which has a paternal effect. In *cdc2* mutant pollen, only one sperm cell, instead of two, is produced. Mutant pollen is viable but can fertilize only egg cell in the embryo sac. The authors found that unfertilized endosperm developed, suggesting that a previously unrecognized positive signal from the fertilization of the egg cell initiated proliferation of the central cell (Nowack et al., 2006). But, the development of such endosperm has been studied only at the early stages of seed development. It should be noted that even during apomixis, the endosperm can develop without fertilization of the central cell (autonomous development), but then there are disturbances in the development of the endosperm, which lead to a delay in the development of the embryo. The available information on the autonomous development of the endosperm in apomicts, many of which are facultative, is extremely incomplete and fragmentary, and there is not enough documented evidence that the endosperm in such apomictic seeds has an autonomous origin.

Fertilization phases and types. Even before the implementation of the sexual process in flowering plants on the stigma, and then in the tissues of the style and ovary, contact occurs between the sporophyte and the male gametophyte. As yet little is known about pollen tube guidance (Yadegari, Drews, 2004). Several studies have described the mechanisms of gametophyte interaction, and also the fertilization process — from pollination to pollen tube acceptance (Mori et al., 2006). It is known that calcium plays an important role in various embryological processes (Hafidh et al., 2016). The features of its functioning during pollen germination and pollen tube growth were studied. It was observed that plasma membrane-localized calcium pumps and copines coordinately regulate pollen germination and fertility in *Arabidopsis* (Li et al., 2018). Sperm dynamics and behaviour during pollen germination, tube growth and sperm release is being studied (Kliwer, Dresselhaus, 2010).

The ways how elements of the male germ unit (non-motile sperm cells) move within the growing pollen tube are being studied. The most hypotheses predict that kinesins and actin cytoskeleton in the pollen tube enable a short movement of specific organelles or contribute to generative cell or sperm cell transport (Xu, Huang, 2020; Cai, 2022). Some authors believe that the vegetative nucleus is actively transported via myosin motors along actin cables while pulling along the sperm cells as passive cargo. They propose that the observed saltatory movement can be explained by the function of kinesins with calponin homology domain (Schattner et al., 2021). There were described several signaling components that regulate actin dynamics in pollen tubes (Zhang et al., 2023).

The mechanisms of gamete interaction are not fully understood. Many of the processes involve conserved mechanisms and proteins. Some of these proteins are highly polymorphic and species-specific, allowing female flower organs to discriminate self from alien pollen grains/pollen tubes to avoid reproductive failure after pollination and fertilization with incompatible gametophytes and gametes, respectively (Bleckmann et al., 2014; Dresselhaus et al., 2016; Shivanna, 2016).

All stages of pollen germination and pollen tube growth (up to the release of sperm from it in the receiving synergid) are controlled by molecular processes (Kanaoka, 2018). Double fertilization mechanisms are very complex and regulated at multiple levels, and it will be a challenge to overcome all steps simultaneously allowing wide hybridization between plant species that presently cannot be crossed. On the basis of physiological and biochemical studies on the interaction of pollen and pollen tubes with the tissues of the stigma, style, ovary, ovule and developing embryo, 3 phases of fertilization are

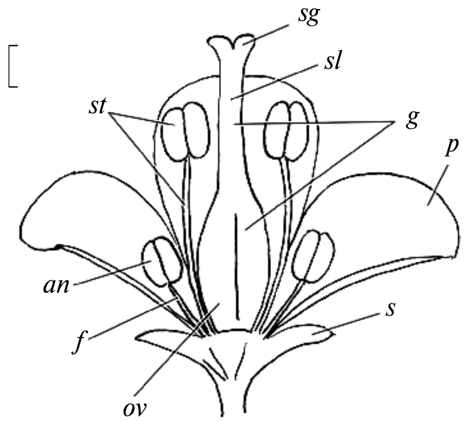

Fig. 6. Flower structure before pollination. *an* – anther, *f* – stamen filiform, *g* – gynoecium, *p* – petal, *ov* – ovary, *s* – sepal, *sg* – stigma, *sl* – style, *st* – stamen. Scale bar, μm: 30.

distinguished (Polyakov, 1970): 1. Progamic phase – lasts until the pollen tubes approach the ovules (usually all processes until the pollen tube enters the embryo sac); 2. Phase of gametogenesis – includes the interaction of pollen tubes with the tissues of the ovule, including double fertilization (this phase is better called syngamic, since gametogenesis, especially male, occurs even before pollination or during the first stages of pollen germination); 3. Postgamic phase – processes occurring after fertilization (the beginning of the development of the embryo and endosperm). Five progamic stages were distinguished involving various prezygotic crossing barriers before sperm cell delivery inside the female gametophyte takes place (Lausser et al., 2010).

For the implementation of fertilization in plants, a transmitting tract of the pistil is created, which is a set of structural elements of the gynoecium, ensuring its interaction with the male gametophyte in the progamic phase of fertilization (Fig. 6). It includes all tissues of the pistil (stigma, style and ovary) with which pollen grains and growing pollen tubes are in contact (Harrisson, 1982; Vishnyakova, 2006). The pollen tube has a dynamic gene expression program allowing it to continuously reset and be receptive to multiple pistil signals as it migrates through the pistil (Palanivelu, Tsukamoto, 2012).

The role of the stigma is to receive pollen. The stigmata differ in morphology (capitate, pinnate) and the structure of the receptive surface: dry (mostly monocots) – covered with papillae cells, wet (mainly dicots) – a secret or secretory mucilage is released on their surface. The styles are open in dicots (hollow, there is a canal), closed in monocots (solid) and half-closed (presence of gynostegium) in Apocynaceae. They lift up the stigmata, that is associated with the characteristics of pollination. In the pistil, the distal part, formed by the upper part of the ovary and style, is called compitum (Shamrov, 2020).

The transmitting tract of the pistil is formed by cells of the secretory type, which secrete various substances (proteins, lipids, polysaccharides) on the surface that are involved in the recognition mechanisms and are a kind of attractants that direct the growth of pollen tubes. To ensure the passage of pollen tubes, specialized secretory tissues arise – obturators. They are localized in various parts of the ovary and ovule and are represented by elongated epidermal cells that grow in the direction of the micropyle and often close the entrance to it. There are various classifications of obturators. Depending on their origin and position in the ovary and ovule, two main types of obturators should be distinguished: 1) ovular – obturators formed from the cells of the ovule; 2) ovarium – formed from ovary cells. Considering the position of the obturators in the ovule or ovary, a number of variants can be distinguished in each type: in the ovular type, integumental, funicular, and nucellar obturators; in the ovarium type, placental, parietal, and septal obturators (Shamrov, 2008).

The role of peptides during the pollen tube journey is being studied – peptide signalling during self-incompatibility, pollen tube growth and guidance as well as sperm reception and gamete activation (Qu et al., 2015). Two types of self-incompatibility are distinguished according to the time of action of genes and the place of localization of their products: gametophytic and sporophytic. In pollen grains, the products of self-incompatibility genes are localized in the sporoderm. In the gametophytic type of control, they come from the microspore protoplast to the intina, later passing into the pollen tube wall created by it, and in the case of sporophytic self-incompatibility, they are localized in the exine (Knox et al., 1975). A well-documented recognition system occurs between pollen grains and the stigma in sporophytic self-incompatibility, where both receptor kinases in the stigma and their peptide ligands from pollen are now known (Lord, Russell, 2002). The products of self-incompatibility genes are glycoproteins. Immunochemical tests have established that the place of their localization in the pistil during sporophytic control of self-incompatibility is the walls of the epidermal cells of the stigma (Kadsamy et al., 1989). In the case of gametophytic self-incompatibility in *Nicotiana alata* Link & Otto (Solanaceae), specific glycoproteins are identified as a component of the intercellular matrix of the transmitting tissue of the style and epiderm of the placenta (Cornish et al., 1987). Self-incompatibility in flowering plants is often controlled by a single nuclear gene (the S-gene) having several alleles. This gene prevents fertilization by self-pollen or by pollen bearing either of the two S-alleles expressed in the style (McClure et al., 1989).

Fertilization processes can be simulated *in vitro* (Kranz et al., 2008). However, they are very complex. Fertilization in flowering plants is a very subtle and accurate process. Compared with animals, in which hundreds of millions of male gametes may target one, often enormous, female gamete, in plants the two nonmotile male gametes target two female gametes with micrometer-level precision (Weterings, Russell, 2004). It is known that in some animals, spermatozoid enters the egg before the completion of meiosis, stimulating it to further development and maturation (Gilbert, 2003). Similar stimulation is observed in plants after pollination. In Orchidaceae, especially primitive representatives, the germination of pollen and the growth of pollen tubes during long flowering causes their ovules to complete the development process and start fertilization (Yeung et al., 1994; Vij et al., 1999). In *Nicotiana tabacum* (Solanaceae), the mature pollen is 2-celled, and the formation of sperm takes place in the pollen tube in the style tissues. The embryo sac at this time is at the 4- or 8-nuclear stage. The embryo sac already after 12 hours acquires a typical structure and is ready for fertilization. In the micropyle, the pollen tube enters 48 hours after pollination (Tian et al., 2005).

The questions of what signals direct the pollen tube to the embryo sac continue to be the subject of debate. Many researchers assign this role to synergids. They play a vital role in the attraction of pollen tubes to embryo sacs, discharge of their contents into them and in ensuring contact and fusion of the discharged sperm cells with female gametes. One view holds that synergids are involved in synthesis and secretion of substances chemotropically active with respect to pollen tubes (Jensen, Fisher, 1968; Plyushch, 1992; Van Went, Willemse, 1984; Higashiyama et al., 2001; Rotman et al., 2003; Punwani, Drews, 2008). However, there is another point of view. The four cell types of the female gametophyte (egg cell, two synergids, central cell, three antipodals) communicate with each other and secrete signaling molecules to guide the male gametophyte and to mediate sperm cell discharge and transport towards the two female gametes (the egg and central cell). After fusion of the gametes, guidance signals have to be removed to prevent polyspermy, embryo and endosperm development is induced generating daughter cells or nuclear regions of a different fate, and cell death is induced in the surrounding ovular cells (Dresselhaus, 2006). Others have expressed a similar point of view. Long-distance pollen tube guidance in *Arabidopsis* is controlled by the 7-celled female gametophyte. But the identification of a central cell guidance (*ccg*) mutant, which is defective in micropylar pollen tube guidance, has shown that expression of CCG in the central cell alone is sufficient to restore the normal pollen tube guidance phenotype, demonstrating that the central cell plays a critical role in pollen tube guidance (Chen et al., 2007). It was demonstrated also that an *in vivo* polyspermy block on the egg, but not the central cell (Scott et al., 2008). It should be emphasized that some authors also noted the signs preventing polyspermy after gamete fusion. In their opinion, after fertilization, the embryo sac no longer attracts the pollen tube, despite the persistence of one synergid cell. This cessation of attraction might be involved in blocking polyspermy (Higashiyama et al., 2001).

In most plants, by the time of fertilization or during it, one of the synergids degenerates. It was demonstrated that synergid cell death in *Arabidopsis* initiates after the pollen tube arrives at the female gametophyte but before pollen tube discharge (Sandaklie-Nikolova et al., 2007). When pollen tube enters one of the synergids, the contents are released through the filiform apparatus. The connection between the sperms and the nucleus of the vegetative cell is lost, and cytoplasmic bodies are formed (Russell, 1992). In *Gossypium* (Jensen, Fisher, 1968), *Zea* (Vazart, 1969), and *Spinacia* (Wilms, 1981), one of the synergids begins to break down even before the entry of the pollen tube. In *Capsella* (Schulz, Jensen, 1968) and *Helianthus* (Newcomb, 1973), both synergids remain intact, and only after the pollen tube enters either of them do changes begin in the ultrastructure of the receptive synergid. Regardless of the time of entry of the pollen tube, in both cases, similar transformations are observed in the structure of the synergids.

Both during premature degeneration and when the pollen tube enters the intact synergid, the changes relate to a decrease in the volume of the cytoplasm, compression of vacuoles, destruction of the plasmalemma, and disorganization of cell organelles. In the synergid, the growth of the pollen tube stops, it bursts, and the sperms are released. The cytoplasm of the pollen tube mixes with the cytoplasm of a degenerating receptive synergid (Dresselhaus, Franklin-Tong, 2013). In *Plumbago zeylanica*, in the absence of synergids, the pollen tube enters the embryo sac from the side of the egg, and the components of the common median cell plate are destroyed, as well as the outer and inner membranes of the pollen tube, both between the sperm and between the egg and the central cell in the area of the emerging extracellular space (Russell, 1983).

The movement of sperm upon entering the embryo sac of flowering plants is carried out with the help of actin. Actin bundles, or actin matrix, are formed in the cytoplasm of the pollen tube. Both sperms migrate with the help of actin to the site of gamete fusion, with one of its branches associated with the sperms, which fuses with the egg, and the other branch is associated with another sperm, which unites with the central cell (Russell, 1992). However, the mechanisms of gamete interaction are not fully understood (Mori et al., 2006; Mori, Igawa, 2014). The question arises, which of the two sperm fuses with the egg, and which with the central cell? Even Nawaschin (1910) suggested that this phenomenon is based on the heterogeneity, or enantiomorphism, of sperms. Fertilization involves a pair of female nuclei (a pair of female cells), one right and one left, and a pair of male nuclei (a pair of sperms), also one right and one left. In his opinion, this system is a necessary condition for the “choice” of the egg and the polar nucleus (central cell) of the corresponding sperm. Investigation of sperms in maize was shown that both male gametes have the capacity to fuse with the egg cell (Faure et al., 2003). When studying the sperm–egg interaction, a novel protein was revealed. It was designated as GCS1 (Generative Cell Specific 1), and was isolated from generative cells of *Lilium longiflorum* Thunb. pollen. Immunological assays indicate that GCS1 is accumulated during late gametogenesis and is localized on the plasma membrane of generative cells. In addition, *Arabidopsis thaliana* GCS1 mutant gametes fail to fuse, resulting in male sterility and suggesting that GCS1 is a critical fertilization factor in angiosperms (Xu et al., 1999; Mori et al., 2006; Twell, 2006).

Subsequently, indeed, in some flowering plants, sperm dimorphism was revealed. Thus, in *Nicotiana tabacum*, the sperm, which is not associated with the nucleus of the vegetative cell, is smaller and fuses with the egg cell, while the larger one unites with the central cell (Yu et al., 1992). In *Torenia fournieri* Linden ex E. Fourn. (Scrophulariaceae), one of the sperms first fuses with the egg. A little later, the second sperm moves to the central cell and is located near the degenerating synergid, which is preceded by the migration of the secondary nucleus from the middle part of the central cell to the micropylar part. After triple fusion, the fertilized nucleus of the primary endosperm cell descends (Higashiyama et al., 1997). This has been observed in other plants as well. In *Galanthus nivalis* L. (Amaryllidaceae), even before the entry of the pollen tube into the embryo sac, the secondary nucleus of the central cell begins to migrate towards the egg apparatus and is opposite the receptive synergid, which will degenerate, and the pollen tube will enter through it. The first of the released sperms fuses with the egg cell, and the second is closed to the secondary nucleus and therefore fuses with the central cell (Erdelská, 1983). In the embryo sac of *Plumbago zeylanica*, in the absence of synergids, the pollen tube enters from the side of the egg. The sperms are arranged diagonally, with the distant sperm fusing first with the egg cell, and then the closest one fusing with the central cell (Russell, 1983). However, in *Arabidopsis thaliana* plants, it was found that the “front” sperm (associated with the vegetative cell nucleus as part of the MGU), as well as the “posterior” (not associated with the vegetative cell nucleus), fertilized both the egg and the central cell with equal probability. It was concluded that sperm isomorphism characterizes the general rule, while their dimorphism is rather an exception (Hamamura et al., 2011).

The genetic and cytological aspects of fertilization in angiosperms are studied (Bleckmann et al., 2014; De Graaf, Dewitte, 2019). In flowering plants, sperms are very small, and the process of fusion of male and female gametes occurs very quickly, so it is not always possible to see them in the contact area. Some reports suggest that fertilization of the egg cell is preferred, which was demonstrated, for example, in mutants of *Cyclin Dependent Kinase A1* (*CDKA A1*), which generate only one sperm-like germ cell (Iwakawa et al., 2006; Nowack et al., 2006). A special study of *Arabidopsis thaliana* plants was carried out using a confocal laser microscope. It made it possible to reveal the retention of sperm cells at the border of female gametes under the action of the HTR10-GFP gene product and on the surface of the egg cell under the action of the GFP-PIP2 gene product. Based on the analysis of the presented illustrations, it can be seen that the sperms are also located diagonally, while the sperm, which is more distant from the place of pollen tube unloading, after passing through the synergid unites with the egg cell, and the second sperm unites with the central cell (Igawa et al., 2013). According to other authors, upon sperm cell arrival at the gamete fusion site the egg cell starts to secrete small cysteine-rich proteins of the EGG CELL 1 (EC1) family. EC1 leads to the relocalization of HAP2/GCS1 from the endomembrane system to the sperm cell plasma membrane and thus activates sperm cells enabling them to fuse with the female gametes (Sprunck et al., 2012). The egg cell appears to require activation itself and calcium may play a key role in this process; this is indicated by a single strong Ca^{2+} to transient in the egg cell associated with pollen tube burst and sperm delivery (Denninger et al., 2014), which thus precedes EC1 secretion. The sperm membrane protein DMP9/DAU2 is involved in interaction of male and female gametes that leads to correct double fertilization (Takahashi et al., 2018).

Even earlier, a mechanism of plasmogamy of sperms and female gametes was proposed, accompanied by the formation of bridges between them, through which the nuclei of sperms and, probably, their cytoplasm pass (Van Went, 1970; Plyushch, 1992). Subsequently, it was shown that the process of plasmogamy includes several stages: 1 – contact of the sperm and the female gamete; 2 – fusion of plasma membranes of gametes; 3 – combination of sperm cytoplasm and female gamete (Igawa et al., 2013).

Studies on the *in vitro* induction of karyogamy with the help of an electric pulse were carried out on isolated male and female gametes of *Zea mays* (Faure et al., 1993). Karyogamy includes three stages of nuclear fusion: 1 – the outer membranes of the nuclear coats are in close contact or contact through the endoplasmic reticulum and then merge; 2 – the inner membranes of the nuclear coats merge and bridges form between the nuclei; 3 – bridges increase and can capture a certain amount of cytoplasm.

Observations of the entry of the pollen tube into the embryo sac and analysis of the structure of the central cell made it possible to suggest that the movement of its secondary nucleus in the direction of the egg apparatus, still in the progamic phase, is a signaling mechanism indicating which of the two synergids will be the receptive (Huang et al., 1993). It should be noted that the above assumption has not yet been confirmed, and the mechanism of selection of the receptive synergid is not clear. The second conclusion that follows from this analysis is that of the female gametes, the egg is the first and preferred for syngamy. After the formation of the zygote, a complete polysaccharide wall is formed, and the access of other sperms to the egg is stopped. It is after this, even if the processes of karyogamy of the nuclei of the egg cell and sperm have not been completed, that the signal for the implementation of the triple fusion and the formation of the primary endosperm cell appears to be received.

In some flowering plants (Amaryllidaceae, *Gossypium*, *Rudbeckia*, *Zea*), hemigamy was found, which is an incomplete sexual process in which sperm enters the egg, but karyogamy does not occur. However, sperm stimulates the egg to embryogenesis. Both the nucleus of the egg and the nucleus of the sperm divide autonomously, subsequently forming a chimeric embryo. Its cells are predominantly haploid, although a hybrid diploid tissue may form at the site of contact between sperm and egg nuclei (Solntseva, 1973, 1979; Battaglia, 1981). That is why hemigamy is proposed to be called gynandroembryony (Battaglia, 1981). Hemigamy is not an obligate feature of plants and depends on environmental factors (temperature, light, soil and air humidity). In *Zephyranthes candida*, it was sometimes observed, while in *Z. macrosiphon* (Amaryllidaceae) it was found in 80% of the ovules in the ovary, while in the rest of the ovules syngamy occurs according to the premitotic type (Vorsobina, Solntseva, 1979).

This phenomenon is close to the secondary modifications of the sexual mode of reproduction: androgenesis, gynogenesis and hybridogenesis (Grebelnyi, 2008). In the case of androgenesis, the incoming sperm nucleus replaces the nucleus of the egg, causing the transformed egg cell to develop. The formation of haploid and dihaploid individuals was found in maize (Tyrnov, 2000) and freshwater bivalves (Grebelnyi, 2008). During gynogenesis, the male gamete penetrates into the egg cell, activates it for morphogenesis, but does not take part in further development or participate to a small extent. Gynogenesis has been found in animals – goldfish, tailed amphibians, and freshwater planaria (Grebelnyi, 2008). In plants, examples of gynogenesis are not known. During hybridogenesis (reverse parthenogenesis, according to Tyrnov, 2000; reverse gynogenesis, in our opinion, since during parthenogenesis sperm does not enter the egg), the offspring develops from fertilized eggs and in many cases consists of females, while their cells bear the signs of both parents. During puberty during oogenesis, paternal chromosomes are eliminated – viviparous fish, "edible" frog (Grebelnyi, 2008). A phenomenon very similar in genetic consequences has been described in *Allium* species (Alliaceae). In *A. ramosum* L. and *A. tuberosum* Rottler ex Spreng., endoreduplication of chromosomes was found during the premeiotic interphase in the megasporocyte or at the earliest stages of meiosis (corresponding to the leptotene or pachytene stages of normal meiosis). As a result of further diplospory, the ploidy of the resulting spores and embryo sacs becomes 4n, and not 2n, as in typical diplospory. Then, by parthenogenesis, tetraploid apomictic plants are formed. Among the progeny of such plants obtained by cross-pollination, dihaploids arose, one of which (KAD2) was a diploid apomict (most diploid plants), and the other was a predominantly diploid amphimict (Håkansson, 1951; Kojima, Nagato, 1992, 1997). Thus, in the course of reproduction, the number of chromosomes was halved to 2n, as was the case in megasporocytes before meiosis in tetraploid plants.

In a number of flowering plants (Podostemaceae), endosperm is not formed during triple fusion due to anomalies (Kapil, 1970). The function of the endosperm is performed by so-called "nucellar plasmodium". It is formed from the cells of the chalazal region of the nucellus. Already at the stage of the 2-nuclear embryo sac, the cells of this zone are disintegrated and a coenocytic symplast gradually appears (Arekal, Nagendran, 1975). In the representatives of the family Trapaceae, there is a loss of the triple fusion process due to a violation of the mechanism of sperm separation: in *Trapa astrachanica* (Flerow) N.A. Winter, one of the sperms is retained in the synergid or extracellular space (Titova, 1988). In *T. natans* L., the central cell is fertilized, but the primary endosperm nucleus becomes hypertrophied and shifts to the chalazal part, contacting the nucellar cells (postament and podium), where proteins and starch accumulate (Titova et al., 1997). In most orchids, syngamy and triple fusion occur without deviation. However, in some species (*Oreorchis patens* (Lindl.) Lindl., *Listera nipponica* Makino, *Calanthe* × *veitchii* R.H. Torr.), the sperm nucleus does not fuse with the nucleus of the central cell. In *Calanthe* × *veitchii*, the polar nuclei are usually autonomous before fertilization and, together with the antipodal nucleus, form a polar-antipodal group, most often located near the zygote (Savina, 1979; Savina, Poddubnaya-Arnoldi, 1990). *Gymnadenia conopsea* (L.) R. Br. and *Listera ovata* (L.) R. Br. have a triple fusion. The resulting large endosperm nucleus is located near the cells of the postament, in which dextrins are found (Shamrov, 2008).

Thus, species with disturbances during triple fusion and without endosperm require additional studies. On the one hand, it is very important to identify redundant mechanisms in the embryo sac that would perform not only a trophic function, but also participate in the provision and distribution of signals that regulate the processes of differentiation and organogenesis of the embryo, as is inherent in the endosperm of the sexual nature of angiosperms (Costa et al., 2014; Chen et al., 2014; Locascio et al., 2014; Doll et al., 2017). In mutants of *Arabidopsis thaliana* (Brassicaceae) it was revealed that before fertilization, auxin is present mainly in the nucellus, while it is not found in the functional megaspore. The auxin gradient determines the specificity of cells in the mature embryo sac. It increases from the antipodal cells to the cells of the egg apparatus, with the greatest accumulation of auxin in synergids (Pagnussat et al., 2009). Cytokinins also play an important role in development (Terceros et al., 2020). In plants with ephemeral antipodal cells, which are involved in the creation of the auxin pool before fertilization, this function after fertilization begins to be performed by chalazal haustoria, providing the development of the embryo with signaling molecules. In plants with long-lived antipodal cells and without chalazal endospermal haustoria, antipodes continue to supply phytohormones to the embryo indirectly through the endosperm, even if the endosperm develops autonomously, as in some forms of apomixis, for example, in the Asteraceae and Rosaceae (Kamelina, 2009). It is possible that the suspensor plays an important role in stimulating the embryo at an early stage of development. Using *A. thaliana*, it was shown that in the suspensor there is a SUS gene (DCL1 allele), which normally stimulates the development of the embryo, starting from the globular stage. However, in a mutant plant, this gene promotes the appearance of an additional embryo from suspensory cells (Gilbert, 2003).

On the other hand, it is possible that anomalies in the process of fusion of the central cell and sperm do not allow the developing embryos to develop to the end. Aberrant seeds are formed. Therefore, extensive detailed studies are required at the population level with the involvement of statistical methods of data processing. One of these works was devoted to the study of lethal deviations in the development of the embryo in *Dactylorhiza fuchsii* (Druce) Soó (Orchidaceae). It was revealed that globular embryos are present in the majority of developing seeds at early stages. However, in the future, various anomalies in their structure are revealed (irregularity of cell divisions, lack of regularities in histogenesis – a total of 12 types of disturbances), which leads to low real seed productivity (Andronova, 2011). Similar results were also obtained for *Orchis purpurea* Huds. both self-pollination and cross-pollination. It was found that a high proportion of non-viable seeds are a consequence of the manifestation of lethal anomalies of embryogenesis (Andronova et al., 2020). In gymnosperms, two sperms from one pollen tube can fertilize eggs in different archegonia. If two sperms enter one egg, then one of them (usually the one that penetrated first) fertilizes the egg, and the other gradually degenerates or, together with the contents of the pollen tube, remains in the upper part of the archegonium. In species with unequal size of sperms, the larger one is usually functional (Singh, 1978; Trenin, 1988). However, in some gymnosperms from the Gnetales (*Ephedra*, *Gnetum*), the second sperm can participate in the formation of an additional embryo (the features of double fertilization in gymnosperms were discussed in detail by us earlier). *Welwitschia* lacks the gnetalean pattern of regular double fertilization, as found in *Ephedra* and *Gnetum*. Both sperms from a single pollen tube involve to yield two zygotes (Friedman, 2015).

The cell wall of the egg in gymnosperms is common to it and to neighboring cells of the lining of the archegonium. In mature archegonium, it has thickenings, and these thickenings are usually wider on the side of the egg than on the side of the sheath cells. A detailed electron microscopic study of the penetration of cytoplasmic elements from the sheath cells into the egg was carried (Corti, Maugini, 1964; Willemse, 1974; Williams, 2009). In the cell wall of the egg there are wide pore fields penetrated by plasmodesmata. Thin sections of the egg cell wall in the area of the pore fields during the maturation of the archegonium are destroyed and united. In these places, individual organelles, whole nuclei of sheath cells, as well as sperm cells from the pollen tube can penetrate the egg (Singh, 1978; Trenin, 1988; Zhang, Zheng, 2016). In the fern *Osmundia japonica* Thunb., at first the fertilization of the entire archegonium occurs, in which enter some spermatozoa. One spermatozoid unites with the egg, and the rest of the spermatozoa are destroyed (Cao et al., 2016).

In flowering plants, after the penetration of the sperm into the egg cell, a complete polysaccharide wall of the zygote is formed, similar to how a hard shell appears in animals after the penetration of the spermatozoid into the egg. Mammals have a rather complex mechanism for regulating the penetration of spermatozoid into the egg. Only one spermatozoid can fertilize an egg without causing developmental anomalies. Assume two blocks of polyspermy. The fast block is electrical, associated with sodium ions, while the resting membrane potential increases. Slow block is physical, due to calcium ions (Gilbert, 2003). In flowering plants, the entry of additional pollen tubes into the embryo sac has been noted by many, but cases of fusion of female gametes with more than one sperm are not always recorded, since this occurs only with deviations. Thus, in *Sternbergia lutea* (L.) Ker Gawl. ex Spreng. (Amaryllidaceae), cases were found when both sperms lingered in the synergid, stopped near the egg, or entered it, while the central cell remained unfertilized (Vorsobina, Solntseva, 1979). U. Grossniklaus (2017) carried out a polyspermy experiment in maize using a mixture of pollens from two genetically distinct male parents. The frequency of polyspermy of the central cell is much higher than that of the egg cell in maize and the results are consistent with a study in *Arabidopsis* (Scott et al., 2008). These results indicate that the polyspermy block is likely weaker in the central cell compared to the egg cell. A comparative analysis of the fertilization mechanisms

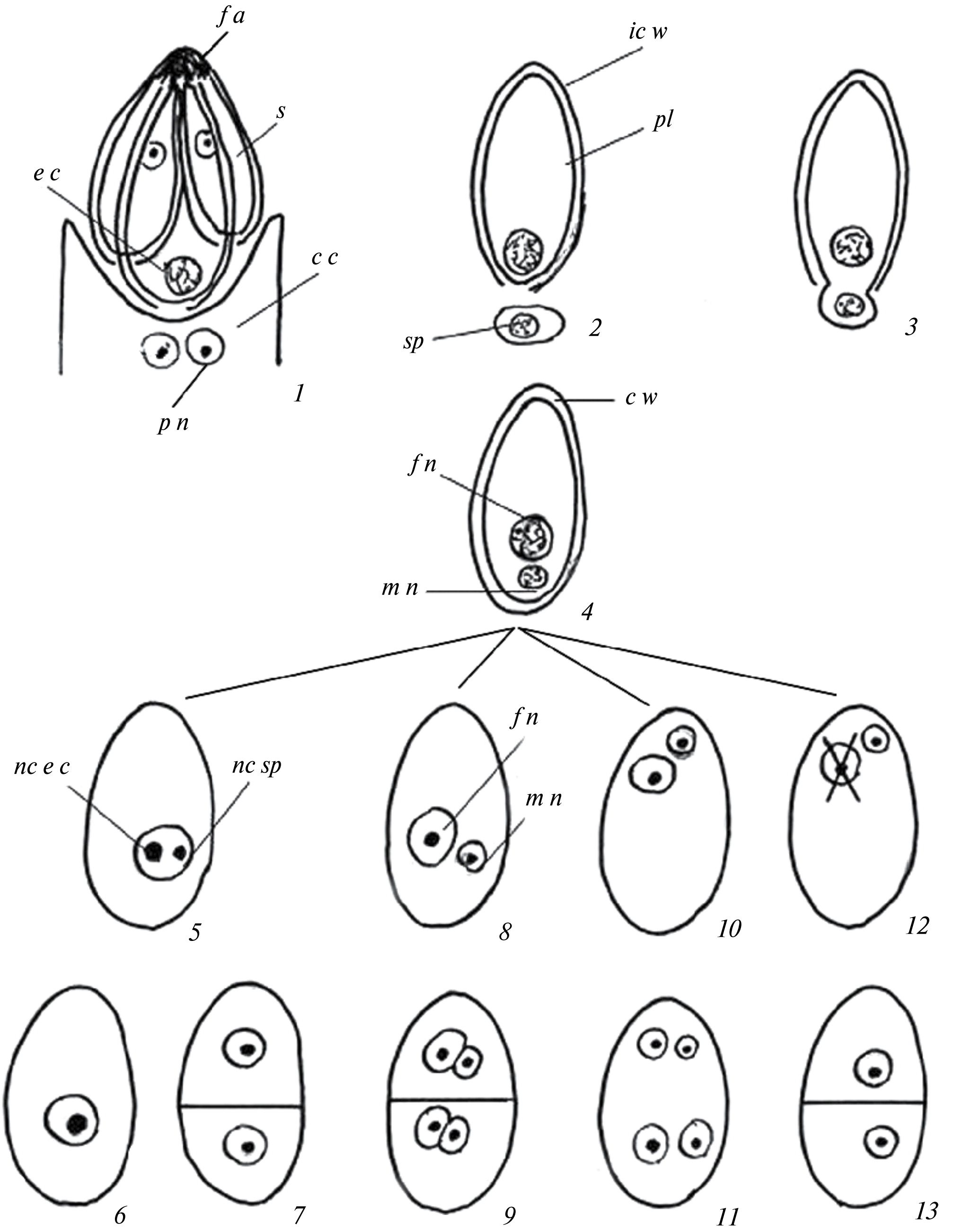

Fig. 7. Fertlization types in flowering plants. *1* – Female Germ Unit (in the apical parts of the egg and synergids, the cell wall is absent; the central cell, synergids, and egg cell in the area of contact with male gametes are covered with a plasmalemma), *2* – sperm is located near the female gamete, *3* – fusion of the plasma membranes of gametes, *4* – plasmogamy is finished, and the cell wall around the developing zygote becomes complete, *5–13* – passage of karyogamy in different fertilization types; complete syngamy: *5–7* – premitotic type: fusion of the female and male nuclei (*4*), release of the nucleoli (*5*), formation of the zygote (*6*) and 2-celled embryo (*7*); *8, 9* – postmitotic type: contact of the female and male nuclei (*8*), and their union at the stage of 2-celled embryo (*9*); incomplete syngamy: *10, 11* – gynandrogamic type: lack of fusion of sex nuclei (*10*), their autonomous divisions (*11*); *12, 13* – androgamic type: replacement of the female nucleus by the male nucleus (*12*) and the formation of an embryo of only paternal origin (*13*). *c c* – central cell, *c w* – complete cell wall, *e c* – egg cell, *f a* – filiform apparatus, *f n* – female nucleus, *ic w* – incomplete cell wall, *m n* – male nucleus, *nc sp* – nucleolus of sperm, *nc e c* – nucleolus of egg cell, *pl* – plasmalemma, *p n* – polar nuclei, *s* – synergid, *sp* – sperm.

in plants and animals has shown that plant synergids are probably also involved in the prevention of polyspermy not only by blocking secretion of further attraction signals but also by gametophyte arrival induced vesicle exocytosis similar to the cortical reaction in animals (Spielman, Scott, 2008).

In *Dioscorea nipponica*, 2 sperms were observed in the central cell. According to the author, the male gametes of one pollen tube did not disperse to different female gametes, but ended up in one, while the egg remained unfertilized (Torshilova, 2018). This was noted during apomixis in some species of *Poa* (Poaceae). These species are characterized by the formation of unreduced embryo sacs and pseudogamy, in which the embryo develops parthenogenetically, and the endosperm develops as a result of fertilization of the central cell. Since the ploidy of the nucleus in the central cell increases by 2 times and becomes 4n, then to achieve the optimal ratio of maternal and parental genomes (2:1), it is necessary to enter two sperms with haploid nuclei into it. Thus, in pseudogamy, both sperms from the pollen tube enter only the central cell, since the sperm is not needed for the parthenogenetic development of the embryo (Yudakova et al., 2018). The entry of both sperms of the pollen tube into the central cell during deviations and the absence of syngamy in the egg cell can be considered as one of the manifestations of the transition from amphimixis to apomixis, especially to parthenogenesis. It should be noted that in lines of *Zea mays* with a high haplo-inducing ability, parthenogenetic haploid embryos develop only after pollination with their own pollen (Apanasova et al., 2017).

As we have already noted, based on a comparison of fertilization processes in flowering plants and animals, two types of fertilization were distinguished: premitotic (Asteraceae, Poaceae, *Scilla*, *Fucus* – plants; sea urchin – animals) and postmitotic (*Lilium*, *Fritillaria*, *Pinus* – plants; roundworm – animals) depending on when the sexual nuclei unite (Gerassimova-Navashina, 1947, 1957, 1969). However, the expediency of such a comparison requires making adjustments and taking into account the specifics of the fertilization process in some plants and animals. It is important to take into account not only the time of fusion of the sexual nuclei, but also the state of male and female gametes in the process of fusion.

First of all, the proposed hypothesis does not fully reveal the differences in the types of fertilization, since it almost does not consider the features of plasmogamy, the first stage of syngamy. In addition, in the English-language literature, the terms “premitotic” and “postmitotic” are practically not used in relation to fertilization. Most often, differences in the rate of fusion of the sexual nuclei are described based on the stages of interphase preceding the division of the zygote, while types of fertilization are equated to types of karyogamy. Thus, Van Went and Willemse (1984), referring to the ideas of Gerassimova-Navashina (1960), describe the types of fertilization as features of the fusion of the nuclei of male and female gametes, while at the postmitotic type, in their opinion, the chromatin of the sexual nuclei remains completely divided before division of the zygote. Some other authors also believe (Faure, Dumas, 2001; Dresselhaus et al., 2016; Ji Min et al., 2020).

However, fertilization includes not only karyogamy, but also plasmogamy (Fig. 7, *1–4*). Based on this, the number of types of fertilization can be increased. In our opinion, hemigamy (gynandrogamic type) and androgenesis (androgamic type) should be added to the classification of types of fertilization. It should be noted that the names of the types (gynandrogamic and androgamic) are a transformed version of the concept “gynandroembryogeny” proposed by E. Battaglia (1981). The angiosperms are likely to have four types of fertilization. These types differ in the degree of completion of syngamy. Premitotic and postmitotic types are characterized by complete syngamy, and androgamic and gynandrogamic types are inherent in incomplete syngamy. Great significance in this case is the behavior of the sperm nuclei. They, as a rule, combine with the nuclei of female gametes (premitotic type – Fig. 7, *5–7*; postmitotic type – Fig. 7, *8, 9*), but the sperm nuclei can remain independent (gynandrogamic type – Fig. 7, *10, 11*) or the female nucleus is replaced by a male one (androgamic type – Fig. 7, *12, 13*).

Based on the mitotic hypothesis and the characteristics of spermiogenesis, it was established (Gerassimova-Navashina, 1947, 1957) that at the premitotic type of fertilization, the fusion of the sexual nuclei occurs before the onset of zygote mitosis. The sperm nucleus in the state of telophase, approaching the female nucleus, is able to “dissolve” the membrane of the latter, sink into it and end its cycle by falling into dormancy, one of the signs of which is the release of the nucleolus (Fig. 8, *1–4*). The zygote, after a certain period of rest, already as a whole, proceeds to the first division (Asteraceae). The second type of fertilization (postmitotic) – the union of the sexual nuclei occurs only in the prophase of the zygote, when both nuclei lose their membranes (the description of the processes is given

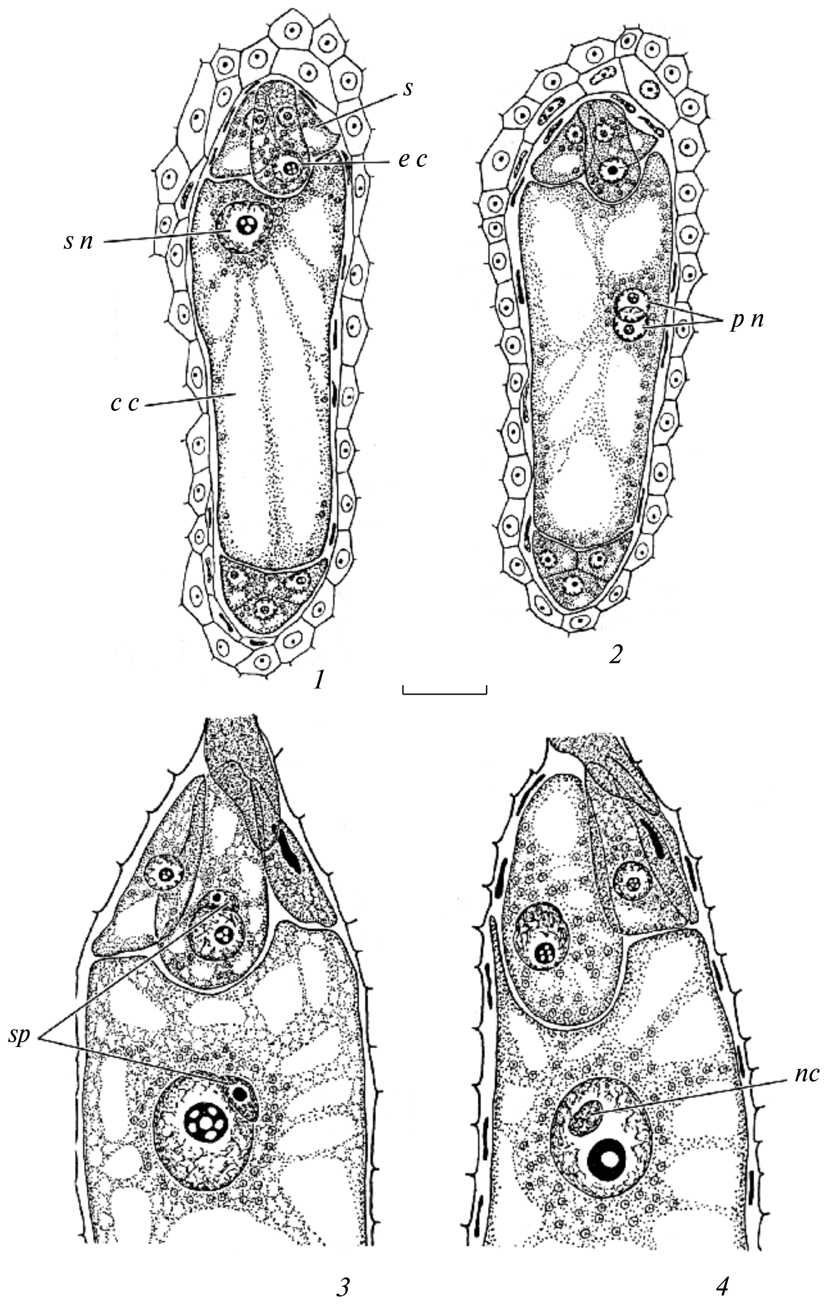

Fig. 8. Formed (*1*) and mature (*2*) embryo sacs, beginning of double fertlization (*3*) in *Ceratophyllum submersum* and completion of this process (*4*) in *C. platyacanthum* (Ceratophyllaceae) (after Shamrov, 1983). *1–3* – bilateral sections, *4* – sagittal section. *c c* – central cell, *e c* – egg cell, *nc* – nucleolus of sperm, *s* – synergid, *s n* – secondary nucleus of central cell, *sp* – sperm. Scale bar, μm: 30.

in the author's version). The state of sperm nuclei included in female gametes was clarified: in the premitotic type, they are in the G_0 or G_1 phases of the interphase cell cycle, in the postmitotic type, in the G_1, S, or G_2 phases (Gerassimova-Navashina, 1969, 1971).

In animals at postmitotic fertilization, the sperm does not come in the mature egg, but enters the oocyte during the first or second divisions at meiosis. In flowering plants, by the time of fertilization, female gametes have already undergone both megasporogenesis and gametogenesis in their development, while synergids begin to release attracting substances in the micropyle, which allows the pollen tube to enter the embryo sac. Consequently, the features in the passage of the postmitotic type of fertilization in plants are hidden not in the specifics of meiosis, as in animals, and not even in the passage of gametogenesis, but, apparently, in the structure of female gametes by the time the pollen tube enters the embryo sac.

Compared with other cells, the greatest differences were found in the structure of the cells of egg apparatus: “pooly differentiated”, “weakly differentiated” and “undifferentiated”. At the same time, such signs as the size, shape, polarity and topography of its elements, the presence or absence of a filiform apparatus in the synergids are considered (Plyushch, 1992).

For fertilization to be successful, the cell cycles of the male and female gametes must be synchronized. Almost all animals undergo gamete fusion in the G_1-phase of the cell cycle (with a 1C complement of genomic DNA). Seed plants appear to be an exception in that they fuse in either G_1 or G_2 in different species (Weterings, Russell, 2004). Pollen may be in G_1-, G_2-, or S-phase at dissemination. There probably also is a signal indicating that sperm and female target cells are at the same receptive cell cycle phase. *Zea mays* and other members of the grass family tend to fuse in G_1, but others may be disseminated in S-phase and complete DNA synthesis in the pollen tube to fuse in G_2, in synchrony with the female target cells (Friedman, 1999).

Based on detailed studies of the content of nuclear DNA in male and female gametes of *Gnetum gnemon* using fluorescence microscopy, three types of karyogamy in seed plants were identified (Carmichael, Friedman, 1995): G_1-karyogamy (gamete nuclei contain 1C DNA during fertilization, and the zygote enters phase of DNA synthesis before mitosis); S-karyogamy (gamete nuclei contain 1C DNA at the beginning of fertilization, DNA replication occurs before the end of the fusion of gamete nuclei); G_2-karyogamy (gamete nuclei go through the S-period of the cell cycle and increase the DNA content from 1C to 2C before fertilization). With established types of karyogamy, DNA replication occurs either still in gametes (G_2-karyogamy), before the end of the fusion of gamete nuclei (S-karyogamy) or after karyogamy, but before the division of the zygote (G_1-karyogamy), i.e. in accordance with the premitotic type fertilization. In *Nicotiana tabacum*, it was shown that if the fusion of gametes occurs in the G_1 phase, then after karyogamy, the S phase and division of the zygote occur. If the gametes fuse in the G_2 phase, then the zygote enters mitosis without additional DNA synthesis (Tian et al., 2005).

Therefore, the premitotic type of fertilization occurs in the same way in animals and plants, as the protoplasts and gamete nuclei combine before the first mitosis of the zygote nucleus (Fig. 7, *5–7*). As for the postmitotic type, it is carried out on a completely different basis. In animals, the spermatozoid enters the developing oocyte during the first or second division of meiosis. It activates the developing egg for further development, then fertilization occurs, but the chromatin of both nuclei condenses into chromosomes that are located separately on a common mitotic spindle, and in mammals with postmitotic fertilization, the diploid set of chromosomes is formed not in the zygote, but at the stage of a two-celled embryo (Gilbert, 2003). It is believed that in flowering plants, gametes and their nuclei unite at mitosis of the zygote nucleus during the formation of the metaphase plate (Gerassimova-Navashina, 1947, 1971). However, the conclusion about nuclear fusion at postmitotic fertilization in plants seems to need to be corrected. Usually the metaphase of zygote division is shown schematically, but there are no detailed pictures of the union of male and female chromosomes. It is possible that at postmitotic type of fertilization in plants, sperm and egg chromosomes do not unite during mitosis. They further divide independently, and the diploid set of chromosomes is created not in the zygote, but in a 2-celled embryo (Fig. 7, *8, 9*). It is with this interpretation of the union of chromosomes of the sexual nuclei that the concept of “postmitotic type of fertilization” acquires its original meaning – the union of the sexual nuclei and the chromosomes included in them occurs after mitosis in the zygote, namely, in the process of cytokinesis and the formation of a 2-celled embryo.

CONCLUSION

Currently, a number of topical directions for the study of gametogenesis and double fertilization in angiosperms can be proposed.

1. When studying fertilization, it is important to characterize not only the features of karyogamy of the sexual nuclei, but also pay attention to the processes occurring during plasmogamy. Therefore, in the classification of types of fertilization into two types (premitotic and postmitotic), it is proposed

to include the phenomena of hemigamy (gynandrogamic type) and androgenesis (androgamic type), which were previously considered within the framework of apomixis forms.

2. The conclusion about nuclear fusion during postmitotic fertilization in flowering plants needs to be corrected. It is possible that in plants, as in animals, the sperm and egg chromosomes unite after the division of the zygote nucleus. Therefore, detailed studies are needed on the state of the nuclei during fusion, during mitosis, and during the formation of a 2-celled embryo.

3. Unlike animals, in flowering plants, the peculiarities in the passage of the postmitotic type of fertilization are hidden not in the specifics of meiosis and even gametogenesis, but, apparently, in the structure of the cells of the egg apparatus, which manifests itself in the incompleteness of the processes of specialization of the egg and synergids by the time of entry of the pollen tubes into the embryo sac. It is necessary to identify the features of stimulation of the cells of the egg apparatus and those cytological mechanisms that ensure the complete unification of the genetic material of the male and female reproductive nuclei during postmitotic fertilization.

4. Particular attention should be paid to those objects in which syngamy can occur, both in the postmitotic and premitotic types.

5. In a number of flowering plants, due to anomalies, endosperm is not formed during triple fusion. Therefore, it is very important to identify duplicative mechanisms in the embryo sac that would perform not only a trophic function, but also participate in the provision and distribution of signals that regulate the processes of differentiation and organogenesis of the embryo, as is inherent in the endosperm of the sexual nature of angiosperms. On the other hand, it is possible that anomalies in the process of fusion of the central cell and sperm do not allow the developing embryos to develop to the end. Aberrant seeds are formed. Therefore, extensive detailed studies are required at the population level with the involvement of statistical methods of data processing.

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СТРОЕНИЕ И РАЗВИТИЕ ГАМЕТ В СВЯЗИ С ОПЛОДОТВОРЕНИЕМ У ЦВЕТКОВЫХ РАСТЕНИЙ

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В статье анализируются данные по процессам, которые происходят до и после оплодотворения у цветковых растений. Гаметы формируются на стадии гаметофита из гаплоидных микроспор и мегаспор. Они представлены спермиями-клетками, яйцеклеткой и центральной клеткой. Слияние мужской и женской гамет происходит после проникновения пыльцевой трубки в любую из синергид. Один спермий сливается с яйцеклеткой, а второй из той же пыльцевой трубки объединяется с центральной клеткой.

У покрытосеменных растений вероятно существуют четыре типа оплодотворения. Эти типы различаются степенью завершенности процесса сингамии. Премитотический и постмитотический типы характеризуются завершением сингамии, в то время как андрогамному и гинандрогамному типам присуща незавершенная сингамия. Важное значение в этом случае приобретает поведение ядер спермиев-клеток. Как правило, они объединяются с женскими гаметами (премитотический и постмитотический типы оплодотворения), однако ядра спермиев могут оставаться автономными (гинандрогамный тип оплодотворения) или ядро женской гаметы после разрушения может быть замещено ядром спермия (андрогамный тип оплодотворения). При премитотическом типе оплодотворения протопласты гамет (плазмогамия) объединяются до начала митоза в ядре зиготы. Что касается постмитотического типа оплодотворения, то он осуществляется на совершенно иной основе. Возможно, что у цветковых растений хромосомы ядер спермия и яйцеклетки не сливаются во время митоза. В дальнейшем они делятся независимо, а диплоидный набор хромосом возникает на стадии 2-клеточного зародыша.

Ключевые слова: мужские и женские гаметы, оплодотворение, сингамия, тройное слияние, типы оплодотворения, покрытосеменные растения

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