

Endosperm development and typification in angiosperms

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Summary: In most classifications, two main types of endosperm development are distinguished: Cellular and Nuclear. The Helobial endosperm is usually considered as a type possessing features of both of these. Some authors add the number of types, or they describe the beginning of endosperm development after one type and the continuation of its development by another type. We propose the original classification of endosperm development modes. It consists of three hierarchical levels – types, subtypes and variations – each of which has its own criteria. The classification includes only two types on the basis of morphogenetic potentialities of the primary micropylar and chalazal cells: Cellular (karyokinesis is completed with cytokinesis in both cells) and Helobial (only karyokinesis takes place in both cells and sometimes the chalazal cell remains uninucleate), a number of subtypes according to the degree of participation of micropylar and chalazal cells in the endosperm construction and a number of variations according to the position of the walls during the second division in the cellular endosperm or the number of nuclei in the chalazal cell of the Helobial type.

In a comparative analysis of flowering plants, the types of embryogenesis are most often derived from the characteristics of the embryo development. As for the endosperm, the types of its development do not correspond to the ‘types’ of embryogenesis, but to a different status. The types of embryogenesis can be compared with subtypes and even variations of the Cellular type of endosperm, while both traits (the contribution of derivatives of micropylar and chalazal cells to the formation of the endosperm; the division patterns of these cells and the form of the tetrad) should be taken into account simultaneously. Apparently, one can also take into account the possibilities of the helobial endosperm – the presence of 2 subtypes and 2 variations.

Keywords: endosperm, development, structure, typification

Until now, the problems of development and typification of the endosperm remain poorly studied, which does not allow us to fully appreciate the significance of the distinguished types for solving many problems of plant development biology. Modern researchers have virtually stopped developing theoretical questions in the field of endospermogenesis. Available literature data require systematisation and rethinking. Let us analyse them not only regarding the typification problem, but also as to some features of the structure and development of the endosperm, starting with the fertilisation process.

Double fertilisation in angiosperms. The endosperm in flowering plants, like the embryo, results from double fertilisation. It involves the union of one sperm with an egg cell (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 double fertilisation phenomenon was discovered in the study of the fusion of female and male gametes in *Fritillaria tenella* and *Lilium martagon*, Liliaceae (NAWASCHIN 1898a, b). At the end of the 20th century, it was shown that it also occurs in gymnosperms of the order Gnetales (*Ephedra*, *Gnetum*) (FRIEDMAN 1990, 1991; CARMICHAEL & FRIEDMAN 1995). However, the question justifiably arises, are the processes of double fertilisation homologous in angiosperms and gymnosperms? In a detailed study, it was found that in *Ephedra nevadensis* and *E. trifurca*, the second sperm cell merges with the abdominal (ventral) tubular cell,

which remains in the archegonial cavity (FRIEDMAN 1990, 1991). An additional embryo forms. Other gymnosperms are similar, but the second embryo does not develop. In gymnosperms, the formation of an additional embryo is more similar to the formation of two embryos in flowering plants, when not only the egg cell is fertilised but also one of the synergids. The synergid can be compared with the abdominal ventral gymnospermous cell, which has a common genesis with the egg cell, since both arise from the same cell. When the egg cell and synergid are fertilised with two sperm cells from the same pollen tube in flowering plants, the possibility of fertilisation of the central cell is lost and without the endosperm, the embryo is destroyed (LAKSHMANAN & AMBEGAOKAR 1984). In *Arabidopsis thaliana* (Brassicaceae) mutants with broken auxin biosynthesis, all cells of the embryo sac can develop either as synergids or as egg cells (PAGNUSSAT et al. 2009), or two egg cells and one synergid are formed in the egg apparatus. After this fertilisation in the latter case, two embryos are formed, and the endosperm does not arise (BERGER & TWELL 2011).

It is known that NAWASCHIN (1898a, b) compared double fertilisation with polyembryony. The same point of view is held by FRIEDMAN (1994, 1995), who believes that in angiosperms, as a result of fertilisation, two embryos arise, one of which gradually begins to fulfill the function of the endosperm. These ideas were developed by him in subsequent investigations (for example, 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' begins to nourish the remaining embryos. This would happen only, if one or several embryos ceased to develop further, and the plant began to use the plasmic substances formed for the final formation of the single embryo. It should be emphasised that the endosperms in angiosperms and gymnosperms, performing a similar function, have a different origin. In gymnosperms, the endosperm is a female gametophyte. One or more peripheral cells in its micropylar part give rise to archegonia. Cells adjacent to the archegonia are transformed into the covering ones. The remaining cells of the female gametophyte turn into storage tissue for the seed during the development of the embryo (TRENIN 1988). A similar nutrient tissue, called perisperm, is formed in flowering plants also after fertilisation due to the accumulation of nutrients in the remaining megasporangium (nucellus) cells of crassinucellate ovule. Perisperm was found not only in the seeds of primitive (Cabombaceae, Cannaceae, Costaceae, Marantaceae, Nymphaeaceae, Zingiberaceae), but also in a number of advanced (Amaranthaceae, Caryophyllaceae, Phytolaccaceae, Portulacaceae) families. Unlike gymnospermous endosperm and angiospermous perisperm, the endosperm of flowering plants does not perform only trophic but also morphogenic functions. It is involved in the provision and distribution of signals regulating the processes of differentiation and organogenesis of the embryo (CHEN et al. 2014). These signals include dipeptides (COSTA et al. 2014) and phytohormones, of 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. It does not give rise to a new organism. Its cells become specialised very early and even *in vitro* culture failed to convincingly prove the occurrence of endospermal embryos (JOHRI & AMBEGAOKAR 1984). The significance of the endosperm that occurs, when the central cell is fertilised with sperm cell, especially becomes relevant in plants with apomixis (primarily cereals). In this case, the parthenogenetic embryo does not start differentiation and histogenesis on its own and it is forced to wait until the endosperm is formed as a result of pseudogamy and starts this process (YUDAKOVA et al. 2018). The significance

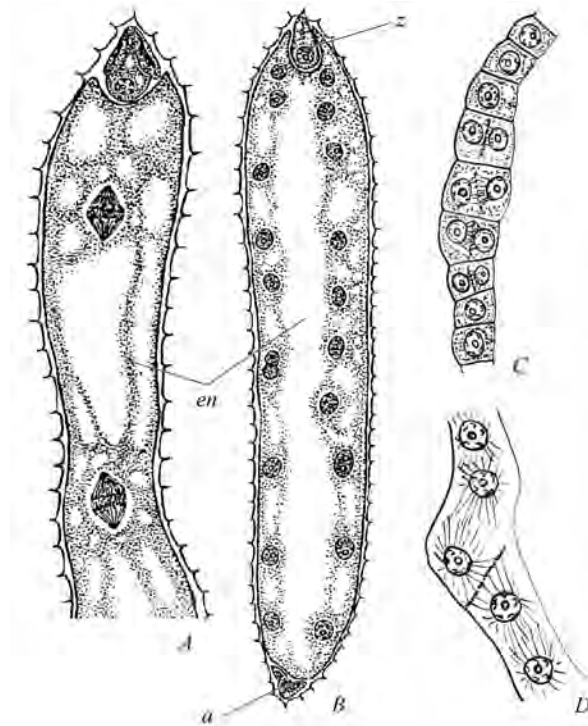


Figure 1. Endosperm structure and development of the Nuclear type in *Gentiana lutea*. Stages of development: coenocytic (A, B) and alveolar (C, D). *a* – antipodals, *en* – endosperm, *z* – zygote.

of the endosperm resulting from fertilisation of the central cell is especially important when considering adventive embryony. 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. The existing endosperm system allows the nucellar and integumentary embryos to enter the cavity of the embryo sac to complete the normal course of development (SHAMROV 2019).

Endosperm types. Endosperm is found in most angiosperms. However, in some plants (Podostemaceae) it is absent (KAPIL 1970). The function of the endosperm is performed by the so-called ‘nucellar plasmodium’. It is formed from cells of the nucellus chalazal region. Already at the stage of the binuclear embryo sac, cells of this zone are disintegrated and a coenocyte symplast gradually appears (AREKAL & NAGENDRAN 1975). In the representatives of Trapaceae and some Orchidaceae, the primary nucleus of the endosperm does not divide, and the endosperm remains unicellular. In *Trapa natans* (Lythraceae), the primary nucleus of the endosperm becomes hypertrophied and moves to the chalazal part in contact with the nucellus cells (postament and podium), in which proteins and starch accumulate (TITOVA et al. 1997). In *Gymnadenia conopsea* and *Listera ovata* (Orchidaceae), the large endosperm nucleus is located near the postament cells, in which dextrans are found (SHAMROV 2008).

In most classifications, two main types of endosperm development in flowering plants are distinguished: Cellular (divisions of nuclei accompanied by cytokinesis) and Nuclear (cell formation delayed until the endosperm becomes multinucleate) (Fig. 1A–D). The helobial endosperm is usually considered a type possessing features of both types; division of the primary

endosperm cell results in formation of two cells, which (typically the micropylar one) later undergo only free nuclear divisions (KHUDYAK 1963; PODDUBNAYA-ARNOLDI 1976; KORDYUM 1978; VIJAYARAGHAVAN & PRABHAKAR 1984). Some authors add a fourth type – Intermediate – along with Helobial (WUNDERLICH 1959) or Tubifloral along with Cellular (KAMELINA 1997).

Nucleus position in primary cell and peculiarities of early endosperm development. The type of the endosperm development is largely determined by the position of the nucleus of the primary endosperm cell. In the Nuclear type, the nucleus is often located in the micropylar part. However, its movement to the middle (Onagraceae, Vitaceae) or chalazal (Capparaceae, Tiliaceae) regions is indicated for a number of plants (ZHUKOVA 1997b). The nuclei, as they divide, are located on the periphery of the emerging coenocyte, edged out by a large vacuole. Next, the process of cellularisation begins. The nuclear endosperm is characteristic of both dicotyledonous and monocotyledonous plants. During the development of the cellular endosperm, the nucleus of the primary cell is most often located in the micropylar or middle (SHAMROV 1997a) parts. Its division is usually transverse, less commonly longitudinal or inclined. In *Adenophora taurica* (Campanulaceae), it is first located in the middle of the central cell, then gradually descends to the chalazal end, where its first division occurs (SHEVCHENKO & KRAINYUK 2019). Cellular endosperm is characteristic of dicotyledonous plants. Data obtained on its development in a number of monocotyledons (Araceae, Burmanniaceae, Lemnaceae) have been questioned (LAWALRÉE 1952; MAHESHWARI & KHANNA 1956; PARAMESWARAN 1959). The same is true for the helobial endosperm, which is inherent in monocotyledons. The results of its description in some dicotyledons (Olacaceae, Santalaceae, Saxifragaceae) have not been further confirmed either (SWAMY & KRISHNAMURTHY 1973). In the Helobial type, the nucleus of the primary cell is usually located near the antipodals (VORSOBINA & SOLNTSEVA 1979; SHAMROV 1997b). During the formation of the helobial endosperm after the first division, two unequal cells are formed: in the large micropylar cell, the formation of a multinuclear coenocyte occurs, and the small chalazal can remain mononuclear or several nuclei appear in it. Then, cell formation begins in the micropylar and sometimes chalazal cells of the helobial endosperm.

In different types of endosperm, the differences in the behaviour of the nucleus of the primary cell and in subsequent development were revealed. So, after formation of two cells in Aquifoliaceae (endosperm of Cellular type of development), subsequent divisions in them may not be accompanied by cytokinesis (HERR 1961), that is, the development of the endosperm begins in the Helobial type. An endosperm of Helobial type of development is typical of representatives of Saxifragaceae, though it can be cellular or nuclear (KOROBOVA-SEMENCHENKO 1977). In species of *Impatiens* from Balsaminaceae (endosperm of Cellular type of development), division of the micropylar cell results in formation of a row of three cells, the upper one of which transforms into a micropylar haustorium, while in the lower and middle cells free nuclear divisions pass (DAHLGREN 1934). The same is observed in Loganiaceae as well (YAMAZAKI 1963). In Acanthaceae, the endosperm formed on the basis of the middle cell can be either cellular (*Acanthus*, *Peristrophe*) or free nuclear (*Barleria*, *Ruellia*) from the very beginning (MOHAN RAM 1962; KARLSTRÖM 1974a, b; MADHAVAN & GUPTA 1982). The endosperm in *Arabidopsis thaliana* (Brassicaceae) is widely accepted as following the Nuclear type of development. However, according to HERR (1999), one nucleus of the binucleate endosperm migrates into the chalazal region and further 2–8 nuclei form, which become enshrouded with dense cytoplasm, creating the effect of a helobial endosperm. A similar feature of endosperm structure and development in this species

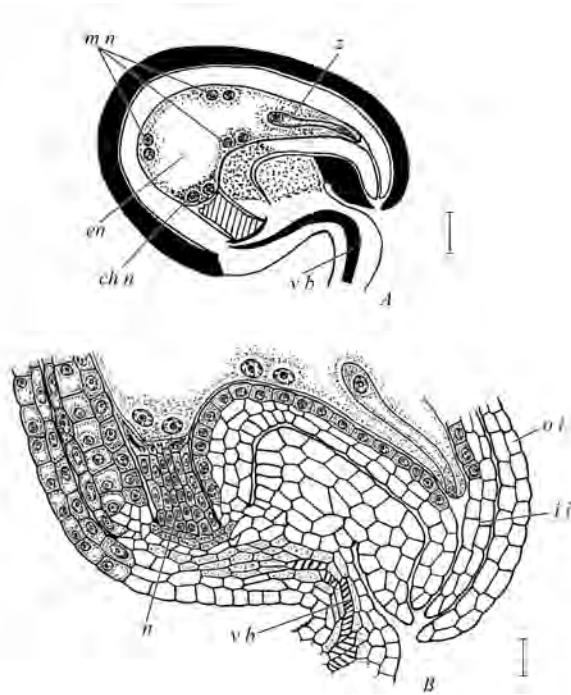


Figure 2. Developing seed at the stage of zygote and first nuclei of endosperm in *Arabidopsis thaliana*. General view of the seed (A), micropylar and chalazal portions of the seed (B). *chn* – chalazal nuclei, *en* – endosperm, *ii* – inner integument, *mn* – micropylar nuclei, *n* – nucellus, *oi* – outer integument, *vb* – vascular bundle, *z* – zygote.

(Fig. 2A, B) and *Capsella bursa-pastoris* was noted by SHAMROV (2002, 2007). In *A. thaliana*, the number of nuclei in the chalazal part was 4, while in *C. bursa-pastoris* it was much larger, with aggregation of nuclei and their polyploidisation. The chalazal nuclei in *A. thaliana* can also fuse, as a result of which they become 2–3 times larger than the nuclei of the micropylar region, while their ploidy increases (BAROUX et al. 2004). The nuclei in the chalazal region of the endosperm gradually degenerate. The functional endosperm is produced by nuclei of the micropylar region.

In *Gagea stipitata* (Liliaceae) (SHAMROV 1999), cell formation in the chalazal part of the endosperm, where large polyploid nuclei form, does not occur. A similar behaviour of the nuclear endosperm was previously described in *Hypericum acutum* (Clusiaceae), when, during early embryogenesis a group of nuclei in the chalazal part of the endosperm are interconnected (STENAR 1938). In *Allium schoenoprasum* (Alliaceae), VINOGRADOVA (2018) revealed several ways to go through the initial stage of development of the nuclear endosperm. After the first division, one nucleus and its derivatives most often remain in the central part of the primary cell (thereof the bulk of the endosperm is subsequently created) and the second migrates to the chalazal part, while the nuclei are larger than the central ones, more chromatised and contain more nucleoli. In the second case, emerging nuclei remain only in the central part of the primary endosperm cell. Very rarely, divisions occur only in the chalazal part, which is typical, as a rule, of the helobial endosperm. A similar fact was noted during the development of the nuclear endosperm in *Dioscorea nipponica* (TORSHILOVA 2018). In *Adenophora taurica* (Campanulaceae), the nucleus of the primary endosperm cell is located in the chalazal end, where the first division occurs. It is transverse with the formation of two unequal cells – the chalazal cell is much smaller than the micropylar. The nucleus of the chalazal cell divides once or twice, slightly enlarges and a small

haustorium forms. This feature of endosperm development is characteristic of the Helobial type. However, the micropylar cell further divides transversely. The endosperm itself is formed from the apical cell, and the basal cell either significantly increases in size or is divided longitudinally and forms a bicellular haustorium (SHEVCHENKO & KRAINYUK 2019).

Peculiarities of Nuclear and Helobial types of endosperm. In the case of the Nuclear and Helobial types, the coenocytic phase is replaced by the cellular one: a cytoplasmic region is separated around each nucleus and a cell wall is formed. Researchers have been studying the genes involved in mitosis and the relationship between the nuclei formed (LIU & MEINKE 1998; LIU et al. 2002; HARA et al. 2015; GUO et al. 2018). At the same time, analysing the state of nuclei during anaphase, which in *Arabidopsis thaliana* (Brassicaceae) is considered to be a critical stage in the cell cycle by synchronising the formed endosperm nuclei, the authors did not correctly call the coenocytic endosperm state as syncytial one (SREENIVASULU & WOBUS 2013; HARA et al. 2015; GUO et al. 2018). First of all, the semantics of the term ‘syncytium’ (Greek *syn* = together, *kitos* = cell) indicates a continuing relationship between the divided cells and not between the nuclei that are formed in the Nuclear and Helobial types. Typical syncytium is known in animals in the form of germinal mesenchyme tissue. In humans, syncytium is formed during spermatogonial divisions. In this case, the cytokinesis does not reach the end and the cells turn out to be interconnected by cytoplasmic bridges (B-group). Subsequent divisions form clones of interconnected cells (GILBERT 2003).

Cells are centripetally formed: first peripheral cells develop and then internal endosperm cells. The initial stages of cellularization are characterised by some features. When the first layer is formed, only radial and external tangential cell walls are formed. The cells of the layer facing the vacuole lack a cell wall and are covered with plasmalemma. This stage of development of the nuclear and helobial endosperm is called alveolar (VAN LAMMEREN 1988; XUHAN & VAN LAMMEREN 1993, 1994). The term ‘alveolus’ was proposed by SOKOLOWA (1890) to denote radially elongated cells that close in the center of the female gametophyte conifers during the transition from the nuclear to the cellular stage of endosperm development. Only after the formation of the cell wall on the inside, cell division begins. Such endosperm in gymnosperms is designated as alveolar (SINGH 1978). In flowering plants, in contrast to gymnosperms, the periclinal divisions occur in its cells after the formation of the first alveolar layer. An epidermal layer is formed, the cells of which have full walls. The underlying layer shows signs of an alveolar structure. This process continues, until the whole vacuole is occupied by cells. In plant species with embryo postdevelopment (Paeoniaceae, Ranunculaceae) beginning from a globular developmental stage, an endosperm cavity forms in the center around the embryo as a result of lysis of the endosperm cells. This cavity becomes more pronounced at the time of seed dispersion (SHAMROV 1997d; BUTUZOVA 2018). In representatives of some families, the endosperm remains nuclear throughout its existence (Cymodoceaceae, Juncaginaceae, Zosteraceae). The number of free nuclear divisions varies among different taxa.

According to the data of electron microscopy, the cell wall of the coenocytic endosperm has numerous outgrowths (VIJAYARAGHAVAN & PRABHAKAR 1984; BHANDARI & ANURADHA MAL 1989). Many plants have such outgrowths in the central cell of the embryo sac (VAZART & VAZART 1966; NEWCOMB 1973), which allows the lateral transport after fertilisation, especially in the presence of an integumentary tapetum.

The direction of the laying of cell walls varies depending on the taxon: it can start from the periphery of the coenocyte and go to the center or from one of the poles of the endosperm and move in the direction of the longitudinal axis to the other pole (usually from the micropylar to the chalazal end). In *Gentiana lutea* (Gentianaceae), cell formation begins upon reaching 128 free nuclei. The first cells are formed near the zygote, then this process is shifted to the middle and lower parts, which leads to asynchronous cell formation. So, in the micropylar part, there are already two layers (corresponding with the stage of a 2–3-celled embryo), while in the chalazal part only the laying of partitions between the nuclei is initiated (Fig. 1A–D) (Shamrov, original data).

The mechanisms of the formation of cell walls between the nuclei of the coenocyte are still subject of discussion: cell formation is carried out by the formation of cell plates (using fragments); in the endosperm, there are cell-forming methods that are not associated with mitosis; cytokinesis initiation is associated with the free centripetal growth of cell walls between the nuclei of the endospermal coenocyte. When studying the localisation of microtubules during the development of the nuclear endosperm of *Coronopus didymus* (Brassicaceae), it was shown that before the onset of cell formation in the peripheral layer, the so-called nuclear-cytoplasmic domains are formed, which are a complex of nuclei and microtubules radially diverging from them (NGUYEN et al. 2002). As a result of the interaction of overlapping microtubules of neighbouring nuclei, additional phragmoplasts are formed, in the center of which cell walls are formed. Using immunocytological studies of microtubules in the nuclear endosperm of *Brassica napus*, it was revealed that their rays from one nucleus interact with microtubules of the neighbouring nucleus (VAN LAMMEREN et al. 1997). In *Gentiana lutea*, they begin to diverge after a critical number of free nuclei is reached, with each core pair remaining close to the wall of the primary endosperm cell, and the other core is shifted inward relative to the first at an angle of 45°. The location of adjacent nuclei resembles a broken line. As a result of this, the necessary space is created for the crossing of microtubules that appear around the nuclei. Radial walls arise between adjacent nuclei (Fig. 1C, D) (Shamrov, original data). A similar mechanism is probably generally biological and supports the formation of microspore tetrads occurring according to the simultaneous type, the formation of cells in the embryo sac and blastomerisation of zygote in animals. In plant cytokinesis, actin is thought to be crucial in cell plate guidance to the cortical division zone. To elucidate actin organisation during cytokinesis, an experimental system was employed. In this system, the mitotic apparatus was displaced and separated from the cortical division zone by centrifugation and a returning movement of the cytokinetic apparatus in cultured-tobacco BY-2 cells occurs. There is an advantage to observe actin organisation clearly during the cytokinetic phase, because more space was available between the cortical division zone and the distally formed phragmoplast (ARIMA et al. 2018).

Typification principles of endosperm. Several criteria are used to distinguish various hierarchical categories of endosperm development:

- 1) occurrence of the cell wall during division of primary endosperm cell (Cellular and Nuclear types);
- 2) position of the first and second cell walls ('types' – MAURITZON 1935; ROSÉN 1949; WUNDERLICH 1967; DI FULVIO 1983; 'forms' – SCHNARF 1917, 1929; GLIŠIĆ 1936–1937; 'variations' – KAPIL & VIJAYARAGHAVAN 1962, 1965; SHAMROV & ZHINKINA 1994);

3) the number of nuclei in the chalazal cell ('forms' in the Helobial type of endosperm development – SWAMY & PARAMESWARAN 1963);

4) position of nuclei in early endospermogenesis ('types' and 'subtypes' in the Nuclear type of endosperm development – DI FULVIO 1983, 1985; DI FULVIO & COCUCCI 1986).

Taking into account the degree of participation of the primary micropylar and chalazal cells in the formation of the cellular endosperm, SAMUELSSON (1913) distinguished two series: series A – both cells participate in the formation of the endosperm and series B – only one of the cells forms the endosperm, while the other cell functions as a haustorium. These features were used in a new general classification of the endosperm in flowering plants (DI FULVIO 1983, 1985; DI FULVIO & COCUCCI 1986). According to this classification, the Cellular type of endosperm development as well as the Nuclear type were designated as megatypes, subtypes as types and variations as subtypes.

In our opinion, the criteria proposed do not entirely reflect the whole specificity of endosperm development. In most classifications, the Helobial type, as an Intermediate one, is neglected, even though it occurs in a considerable number of taxa of flowering plants. Some authors do not consider it as an independent one and include it in the Nuclear type (SPORNE 1954, 1967) or in the Cellular type (SWAMY & GANAPATHY 1957). Only a few papers have noted the significance of the Helobial type in the evolution of the endosperm. HERR (1999) supposed that the Helobial type might not be viewed as an intermediate step in derivation of cellular from nuclear endosperm, but rather as a parallel evolutionary event. MAHESHWARI (1950) had already pointed to the imperfection of the classifications of the types of endosperm development, as there were transitional forms among different types. According to TERYOKHIN (1996), in deciding this question, it is important to consider that the mode of endosperm development, as an evolutionary labile structure with various haustorial formations peculiar to it, is bound to adaptive features of seed germination.

Understanding the problem of endosperm typology is quite impossible without taking into consideration the peculiarities of evolutionary appearance of various modes of its development. This forced us to review the idea of principles of endosperm typification and to reconsider the existing diversity of types and variations with respect to data on evolutionary reformations. As a principle of the hierarchical classification of the endosperm development modes, we have chosen that approach (onto-phylogenetic), which does not allow only typification of modes of endosperm formation but also an explanation of their initiation in flowering plants.

The classification proposed consists of three hierarchical levels: types, subtypes and variations, each of which has its own criteria (see Figs 3; 4). The principle of its construction as a whole is similar to that in the identification of types and variations of embryogenesis (JOHANSEN 1950). However, these systems are very different. We will discuss this issue in detail later. In our classification, the following criteria are taken into account: morphogenetic potentialities of primary micropylar and chalazal cells, the degree of their participation in the construction of the endosperm of the seed, the position of the cell walls or the number of nuclei after the second and subsequent divisions and definitive structural organisation.

The characteristic feature of endosperm development in a considerable number of plant species is that the first nuclear division in the endosperm is followed by formation of two primary cells – micropylar and chalazal. As a basis for distinguishing the types, the first consideration concerns

the morphogenetic potentialities of the primary micropylar and chalazal cells of the endosperm expressed in the processes of cyto- and karyokinesis. Then, considering which of these processes is dominant in the period of early endospermogenesis, we propose to distinguish two **main types of development**: **Cellular** (karyokinesis is completed in both cells with cytokinesis) and **Helobial** (only karyokinesis takes place in both cells and sometimes the chalazal cell remains uninucleate). The Nuclear type is considered a subtype of the Helobial type of endosperm development.

Each type is subdivided into a number of subtypes according to the degree of participation of the micropylar and chalazal cells in constructing the endosperm. The following **subtypes** are distinguished in the **Cellular type**:

Micropylar with chalazal haustorium: endosperm forms from the micropylar cell, and the chalazal cell functions as a haustorium (some Icacinaceae, Fouquieriaceae, Saururaceae and many of Hydatellaceae, Nymphaeaceae);

Micropylar with terminal haustoria: endosperm forms out of lower derivatives of the micropylar cell, while the chalazal cell as well as the upper derivatives of the micropylar cell form the micropylar and chalazal haustoria (Buddlejaceae, Crassulaceae, Gesneriaceae, Orobanchaceae, Pedaliaceae, Plantaginaceae and many Scrophulariaceae and Verbenaceae);

Micropylar-chalazal without haustoria: both cells participate in the formation of the endosperm (Annonaceae, Aristolochiaceae, Ceratophyllaceae, Degeneriaceae, Monimiaceae, Nelumbonaceae, Sarraceniaceae, Winteraceae);

Micropylar-chalazal with terminal haustoria: both cells of the two-celled endosperm form the endosperm and the micropylar and chalazal haustoria (Callitrichaceae, Ericaceae, Lentibulariaceae, Lobeliaceae, Stylidiaceae, some Campanulaceae);

Chalazal with micropylar haustorium: micropylar cell becomes a haustorium, while the chalazal forms the endosperm (Loasaceae, some Campanulaceae, Lamiaceae, Scrophulariaceae).

It is also possible to single out another subtype **Chalazal without haustoria**: only the chalazal cell participates in the formation of the endosperm (Austrobaileyaceae).

In each subtype of the Cellular type, a number of **variations** (for authors who proposed the variations see SHAMROV 1997a,b) can be distinguished according to the position of the walls during the second division in the endosperm.

Micropylar with chalazal haustorium subtype: *Nymphaea*-variation (variation name proposed here). Divisions occur in the micropylar cell in different directions, and the chalazal cell functions as a haustorium (Fig. 3A).

Micropylar with terminal haustoria subtype: *Prunella*-variation. Longitudinal division passes only in the micropylar cell and a T-shaped triad of cells forms (SCHNARF 1929); *Galeopsis*-variation (SCHNARF 1917), *Alectorolophus*-, *Limosella*-, *Linaria*- and *Veronica*-VI-variations (GLIŠIĆ 1936–1937) are included (Fig. 3C, a); *Callitriche*-variation. Transverse division takes place in the micropylar cell and the linear triad of cells appears (JÖRGENSEN 1923); *Incarvillea*-variation (MAURITZON 1935) and *Stachys*-variation (SCHNARF 1917) are included (Fig. 3C, b).

Micropylar-chalazal without haustoria subtype: *Annona*-variation. Division in both cells form transverse and linear tetrad of cells (SCHNARF 1929); *Ceratophyllum*-variation (SCHNARF

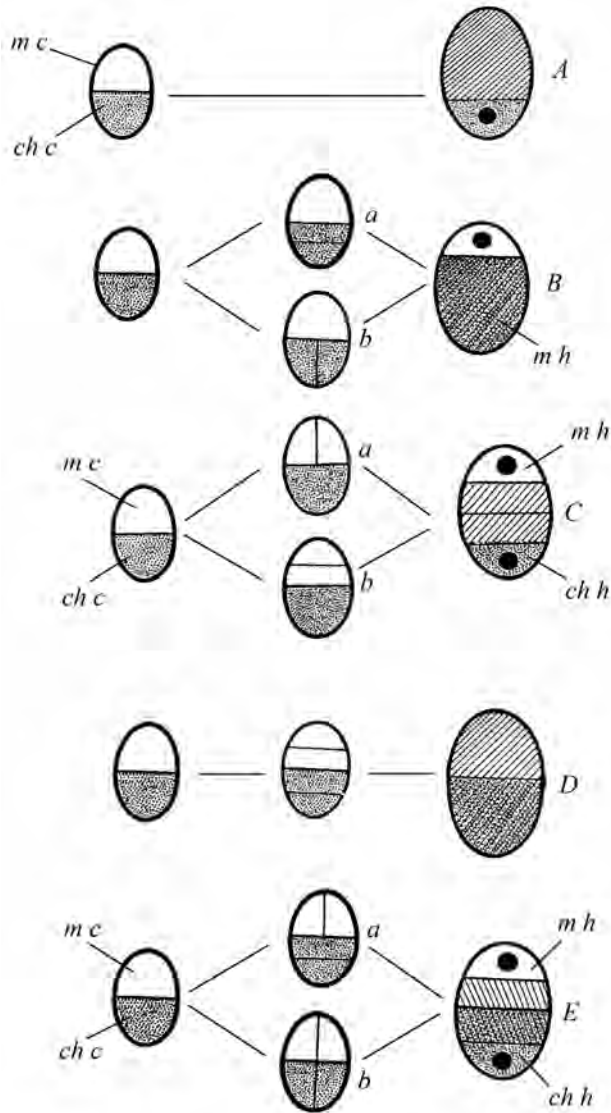


Figure 3. Cellular type and its subtypes and variations. A – Micropylar with chalazal haustorium subtype: *Nymphaea*-variation; B – Chalazal with micropylar haustorium subtype: a – *Pedicularis*-variation, b – *Pentaphragma*-variation; C – Micropylar with terminal haustoria subtype: a – *Prunella*-variation, b – *Callitriche*-variation; D – Micropylar-chalazal without haustoria subtype: *Annona*-variation; E – Micropylar-chalazal with terminal haustoria subtype: a – *Phyteuma*-variation, b – *Scutellaria*-variation. *chc* – chalazal cell, *chh* – chalazal haustorium, *mc* – micropylar cell, *mh* – micropylar haustorium.

1929) is included; as derivative variations; *Adoxa*- and *Lappula*-variations, characterised by longitudinal or a variable laying of the first and a number of subsequent partitions at the early stages of endospermogenesis (SCHNARF 1929), can be attributed here (Fig. 3D).

Micropylar-chalazal with terminal haustoria subtype: *Phyteuma*-variation. Micropylar cell divides longitudinally and chalazal cell undergoes transverse division, which leads to formation of the T-shaped quaternion of cells (ROSÉN 1949); *Isotoma*-variation (ROSÉN 1949) is included (Fig. 3E, a); *Scutellaria*-variation. Division in both cells is longitudinal and accompanied by formation of the isobilateral tetrad of cells (SCHNARF 1917, 1929);

Catalpa-variation (GOVINDU 1950), *Codonopsis*- and *Sphenoclea*-variations (ROSEN 1949), *Prolimosella*-, *Verbascum*- and *Veronica* I–V-variations (GLIŠIĆ 1936–1937) are included (Fig. 3E, b). This also includes *Ericaceae*- (SCHNARF 1929) and *Azorina*- (SHAMROV & ZHINKINA 1994) variations, the independence of which is questionable. A feature of these variations is that the first stages of endospermogenesis follow the *Annona*-variation (linear tetrad of cells). However, the fate of the derivatives of micropylar and chalazal cells (the formation of terminal haustoria) makes it possible to consider them as part of the Micropylar-chalazal with terminal haustoria subtype.

Chalazal with micropylar haustorium subtype: *Pedicularis*-variation. Chalazal cell divides transversely, which results in the formation of a linear triad of cells (SCHNARF 1917, 1929); *Lavandula*-variation included (POLYSHCHUK & DZEVALTOVSKY 1971) (Fig. 3B, a). *Pentaphragma*-variation. Division in the chalazal cell is longitudinal and the triad of cells is inversely T-shaped (KAPIL & VIJAYARAGHAVAN 1962, 1965) (Fig. 3B, b).

In the subtype Chalazal without haustoria, variations cannot be distinguished (FLOYD & FRIEDMAN 2000, 2001).

Two subtypes can be singled out in the **Helobial type**:

Micropylar with chalazal haustorium: endosperm formed out of the micropylar cell, while the chalazal transforms into a haustorium (Aponogetonaceae, Asphodelaceae, Costaceae, Hydrocharitaceae, Limnocharitaceae, Phormiaceae, Pontederiaceae, Potamogetonaceae, Ruppiaceae, Zannichelliaceae and some Cabombaceae and Nymphaeaceae);

Micropylar without haustoria (Nuclear subtype): falling out of the first nuclear division, in consequence of which only karyokinesis is carried out during early endospermogenesis (Brassicaceae, Cactaceae, Cyperaceae, Eriocaulaceae, Fabaceae, Gentianaceae, Poaceae, Restionaceae, Rosaceae, Zosteraceae).

In the **Micropylar subtype of the Helobial type**, two variations are distinguished according to the number of nuclei in the chalazal cell of the two-celled endosperm: ***Limnocharis*-variation** (variation name proposed here) (A-form according to SWAMY & PARAMESWARAN 1963; uninucleate according to SHAMROV 1997c) (Fig. 4A, a) – Aponogetonaceae, Hydrocharitaceae, Limnocharitaceae, Potamogetonaceae, Ruppiaceae, Zannichelliaceae and some Cabombaceae, Nymphaeaceae) and ***Dianella*-variation** (variation name proposed here) (B–E-forms according to SWAMY & PARAMESWARAN 1963; polynucleate according to SHAMROV 1997c) (Fig. 4A, b) – Asphodelaceae, Costaceae, Phormiaceae, Pontederiaceae, Typhaceae. In the Micropylar without haustoria subtype, the singling out of variations is difficult (Fig. 4B), since there are no clear criteria for their separation. Some authors (ROSEN 1927), depending on the mode of transition of the free-nuclear stage of development to the cellular, distinguish several types (variations) of cellularisation in the endosperm.

Possible evolutionary trends of endosperm development. The appearance of existing modes of formation of endosperm proceeded in relation to the character of development of the surrounding tissues of the ovule and seed. The interrelations between endosperm and embryo on the one hand and antipodals on the other, must have been highly significant like the specificity of transport of nutrients in the ovule and seed, which carried on through the system of sequentially functioning haustorial structures.

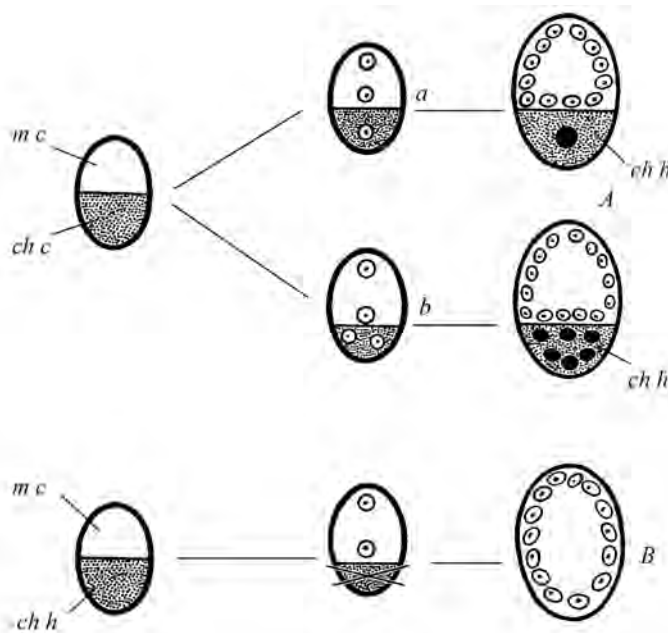


Figure 4. Helobial type and its subtypes and variations. A – Micropylar with chalazal haustorium subtype: a – *Limnocharis*-variation, b – *Dianella*-variation; B – Micropylar without haustoria subtype. *chc* – chalazal cell, *chh* – chalazal haustorium, *mc* – micropylar cell, *mh* – micropylar haustorium.

Evidently, evolution of the endosperm of flowering plants proceeded in several directions. Distribution of types of endosperm in plants is the first evidence of this fact. The Helobial (34 families) and Nuclear (30 families) types of endosperm development are typical of monocotyledons, whereas Nuclear (156 families) and Cellular (135 families) types are typical of dicotyledons (KAMELINA 1991). However, in primitive monocotyledons the endosperm is mostly helobial and less commonly nuclear, while in advanced monocotyledons only the Nuclear type of endosperm is found. A combination of cellular and nuclear endosperm was quite common in primitive dicotyledons, while in advanced taxa either the Nuclear type or the Cellular with haustoria type are observed.

Evolutionary transformations in endosperm development of flowering plants are still being debated (MAHESHWARI 1950; WUNDERLICH 1959; BHATNAGAR & SAWHNEY 1981; DAHLGREN 1991; TERYOKHIN 1996; ZHUKOVA 1997a, b). The initial type is considered to be Nuclear (SCHNARF 1929; SPORNE 1954; PODDUNNAYA-ARNOLDI 1976; BATTAGLIA 1980; VIJAYARAGHAVAN & PRABHAKAR 1984; KAMELINA 1991) or Cellular (COULTER & CHAMBERLAIN 1903; SWAMY & GANAPATHY 1957; BHATNAGAR & SAWHNEY 1981; FRIEDMAN 1994, 1995). There is also an opinion that both types of endosperm development appeared simultaneously (PALM 1915; KORDYUM 1978).

In our opinion, the endosperm development which has been characterised by features of the Cellular and Helobial types (presence of 2-celled stage after division of the primary endosperm cell, simultaneously with interconnected processes of karyo- and cytokinesis or only karyokinesis passing in the micropylar cell) should be considered as the initial type (Fig. 5A). Such a peculiar development of the endosperm was noted in representatives of a number of families, and these examples were discussed earlier. Various types of formation are described in Nymphaeaceae,

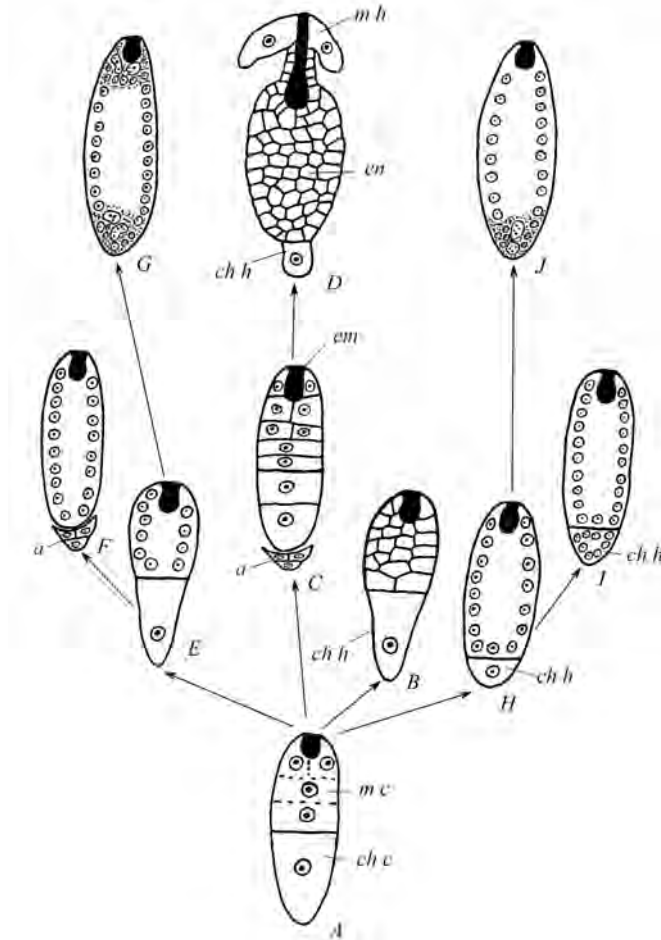


Figure 5. Scheme of possible evolutionary trends of endosperm in flowering plants (explanation in the text). *a* – antipodals, *chc* – chalazal cell, *chh* – chalazal haustorium, *em* – embryo, *en* – endosperm, *mc* – micropylar cell, *mh* – micropylar haustorium.

located at the base of most phylogenetic systems and combining the signs of dicotyledonous and monocotyledonous plants in its structure. Three types of endosperm development were found in the representatives of this family, while the presence of cellular endosperm (the majority of species; BATYGINA & SHAMROV 1985) tends to be dicotyledonous, while the tendency of some representatives to the formation of Helobial (*Nymphaea stellata*; KHANNA 1967) and Nuclear (*Euryale ferox*; KHANNA 1964) types of endosperm is closer to monocotyledons. The Helobial type of development of the endosperm was also found in representatives of the closely related Cabombaceae (BATYGINA & SHAMROV 1985), which are included in the order Nymphaeales like Nymphaeaceae (APG III 2009).

It should be noted that representatives of Hydatellaceae are also included in Nymphaeales on the basis of molecular genetic data (STEVENS 2007; APG IV 2016). First of all, a monosporic, unipolar, 4-celled embryo sac was found in them (RUDALL et al. 2008), as it was revealed earlier in *Nuphar*, *Nymphaea* and *Victoria* from Nymphaeaceae (WINTER & SHAMROV 1991a, b). A similar type of development of the embryo sac predominates in Austrobaileyales (FRIEDMAN et al. 2003; TOBE et al. 2007). Later, it was revealed that the formation of a cellular endosperm with a chalazal

haustorium and the presence of perisperm and operculum in the seed are characteristic not only of Nymphaeaceae, but also of Hydatellaceae (RUDALL et al. 2009). According to these authors, the early endosperm structure in *Trithuria* (Hydatellaceae) and water lilies, namely the presence of a chalazal haustorium, resembles the helobial endosperm of many monocots. In comparison with them, and a similar development of the embryo sac in representatives of Austrobaileyales, the endosperm of the seed is not formed due to derivatives of the micropylar cell, but because of the chalazal cell with no haustorium (FLOYD & FRIEDMAN 2000, 2001).

The endosperm of dicotyledons closest to the ancestral type of development is the Cellular one (for example, Fouquieriaceae, Saururaceae and many Nymphaeaceae) which forms as a result of divisions of the micropylar cell of the two-celled endosperm, while the chalazal cell transforms into a haustorium (Micropylar with chalazal haustorium subtype) (Fig. 5B). Such mode of formation of the endosperm, which is characterised by a high degree of specialisation of the chalazal cell from the first stages of development, has probably appeared to be a deadlock line of evolution. In our opinion, it was the endosperm formed due to divisions of both cells (primary micropylar and chalazal ones) that was of a greater evolutionary significance. It was characterised by a lesser degree of tissue differentiation and the absence of such specialised structures as haustoria (Micropylar-chalazal without haustoria subtype) (Ceratophyllaceae, Monimiaceae, Nelumbonaceae, Winteraceae). In this case, absence of haustoria is compensated by formation of large, long remaining antipodals which participate in supplying a growing endosperm with nutrients at the first stages of development (Fig. 5C). Later, the endosperm with terminal haustoria could have formed on this basis. Either upper derivatives of both cells transformed into haustoria (Micropylar-chalazal with terminal haustoria subtype: Campanulaceae, Lentibulariaceae, Lobeliaceae) or of only the micropylar cell (micropylar with terminal haustoria subtype: Gesneriaceae, Orobanchaceae, Plantaginaceae, Scrophulariaceae) (Fig. 5D). On the basis of the endosperm belonging to the Micropylar-chalazal without haustoria subtype, the endosperm of a number of advanced taxa could also appear, characterised by a longitudinal or variable laying of the first and sometimes a number of subsequent cell walls, from transverse through oblique to longitudinal (some Adoxaceae, Asteraceae, Boraginaceae, Chloranthaceae, Diapensiaceae, Dipsacaceae, Piperaceae, Valerianaceae).

In dicotyledons, the endosperm of Nuclear type development has presumably appeared as a result of gradual reduction of the chalazal cell, whose function has been maintained by other structures (Fig. 5E, F). Initially formation of the endosperm passed without specific haustorial structures being shaped, which is a characteristic, for example, of a number of taxa at the bottom of the flowering plants' system (Casuarinaceae, Myricaceae, Myristicaceae, Ranunculaceae, some Hamamelidaceae, Papaveraceae and other families). Further evolution was associated with heteromorphism of the endosperm and its micropylar and chalazal regions functioning as haustoria (Fig. 5G). Denser cytoplasm and aggregation of nuclei, often hypertrophied and polyploid, are observed either only at the chalazal (Aizoaceae, Gentianaceae, Polygonaceae, Rosaceae, Sapindaceae and other families) or at both poles (Brassicaceae, Caricaceae, Sterculiaceae and other families). Thus, no cellularisation can pass at the chalazal pole, which later leads to the formation of a multinucleate chalazal haustorium (Amaranthaceae, Elaeagnaceae, Fabaceae, Nyctaginaceae, Rhamnaceae). Representatives of Caryophyllaceae, for example, are characterised by a net of haustoria spread over the surface of the endosperm (ROCÉN 1927; TURSSUNOV & SAVINOVA 1979). A correlation can be traced between the presence of haustoria in the endosperm

of the Nuclear type of development and the longevity of antipodals. In plants with antipodals that remain for a long time, the endosperm does not form haustoria, while in the case of ephemeral antipodals, haustoria, first of all the chalazal one, appear.

When discussing the directions of the endosperm evolution in monocots, we note the Alismatales order, in the species of which all types of endosperm are found. This order is very extensive and includes 14 families (APG IV 2016). It is believed that its representatives, mainly Araceae, gave rise to a number of orders: Acorales (one family Acoraceae) and Petrosaviales (one family Petrosaviaceae). In *Lysichiton*, *Orontium* and *Symplocarpus* from Orontioideae subfamily (basal of Araceae), in contrast to the previously existing data on the nuclear endosperm, it was revealed that the endosperm is cellular (TOBE & KADOKAWA 2010). In *Acorus* (a sister group for the other monocots), the appearance of a cellular endosperm correlates with the presence of large antipodes (RUDALL & FURNESS 1997) and the absence of a chalazal haustorium in the endosperm (FLOYD & FRIEDMAN 2000). Comparative analysis with other related monocots showed that the sign of the presence of cellular endosperm is plesiomorphic for Alismatales, Acorales and Petrosaviales. Evolutionary transformations of the endosperm occurred in them twice, from the cellular to the nuclear mode: once they touched the Alismatales and a second time the nuclear endosperm appeared as a synapomorphic trait in the 8 remaining orders of monocots, including Dioscoreales, Liliales, Asparagales and Poales. The helobial endosperm affected all monocots and emerged independently (TOBE & KADOKAWA 2010).

In monocotyledons at the base of the initial type in the micropylar and sometimes in the chalazal cell of the two-celled endosperm, processes of karyokinesis mainly pass (without cytokinesis). So, the Helobial type of endosperm had originally a preferred development (Fig. 5H, I). Its further evolution apparently proceeded in the direction of gradual reduction of the chalazal cell of the two-celled endosperm and establishment of the nuclear mode of its development (Fig. 5J). This is proved, for example, by the presence of both types of endosperm development in a number of families (Alismataceae, Amaryllidaceae, Asparagaceae, Liliaceae, Melanthiaceae and other families). The whole chalazal pole of the nuclear endosperm provides the haustorial function of the chalazal cell or long-functioning antipodals (DE VOS 1949). In the chalazal part of the endosperm of a number of taxa (Iridaceae, Juncaginaceae, Najadaceae, Zosteraceae and other families) with denser cytoplasm and aggregation of nuclei, often of irregular shape, a haustorium is formed sometimes (Areaceae, Commelinaceae and other families). Appearance of the nuclear endosperm in monocotyledons correlates with the general reduction of the ovule (decrease of massiveness in direction from crassinucellate to tenuinucellate ovule and formation of two-layered integuments) (SHAMROV 1997e, 1998, 2000, 2008).

Comparative analysis of classifications of the embryo and endosperm development types. As we have already noted, the principles of classifying the types of development of the embryo and endosperm are generally similar. However, there are significant differences between these systems, especially in terms of assessing the level of the hierarchy (types, subtypes and variations) for the purposes of taxonomy and phylogeny.

The classification of types of embryo development used in literature (JOHANSEN 1950) is a transformed version of previously existing classifications. CARANO (1915) proposed a differentiation of two types for the first time: Cruciferae-type (embryogenesis of *Capsella bursa-pastoris*) and Asteraceae-type (embryogenesis of representatives of the family Asteraceae).

These types are distinguished based on the structural features of the four-celled embryo and the sequence of cell divisions in the course of further development. Later, CHIARUGI (1925), proposed the need to isolate two more types on the basis of the specific structure of the tetrad of embryo cells as well as the degree of involvement of the apical and basal cells in the embryo construction: Solanaceae- and Chenopodiaceae-types. In the latter, he included embryogenesis of representatives of Caryophyllaceae. SCHNARF (1929) gave a different interpretation of the criterion regarding the participation of the basal cell in the construction of the embryo. In the types proposed by CHIARUGI (1925), the basal cell takes part in the formation of the organs of the embryo. Since the basal cell of the representatives of Caryophyllaceae is not involved in this process, SCHNARF (1929) suggested to isolate its development into the original Caryophyllaceae-type. A total of 5 types of embryo development are presented in the classification, while zygote division occurs in the transverse direction. JOHANSEN (1950) changed the names of the types of embryogenesis and supplemented the classification with the Piperad-type (this type is still poorly understood and its comparative analysis with other types is very difficult), in which the zygote is divided longitudinally.

The Paeoniad-type (YAKOVLEV 1958) was also distinguished, which is characterised by the coenocyte state of the embryo in the early stages and the formation of a coenocyte-cellular structure (several embryo-like structures are formed). One of them develops into a well differentiated embryo. It is possible that such embryo development occurs parthenogenetically, since in *Paeonia lactiflora* during the development of multiple archesporium, the megasporocytes in the chalazal part of nucellus undergo normal megasporogenesis, while other megasporocytes in the micropylar part become the initials of diplosporous embryo sacs. Most embryo sacs degenerate during their development. One embryo sac of unknown nature remains (with or without meiosis), in which the egg cell without fertilisation possibly develops by parthenogenesis (SHAMROV 1997d). Pollen tubes were observed in the micropyle and the egg apparatus, but, in *Paeonia*, the phenomenon of pseudogamy (fertilisation of the central cell with sperm-cell and the formation of the primary endosperm cell) seems to occur. Another Graminad- or Poad-type was isolated for monocotyledons and some dicotyledons based on the inclined position of the cell walls in the early period of embryo formation and the specifics of its organogenesis at subsequent stages of development (BATYGINA 1974).

At the present stage of embryology development, the system of JOHANSEN (1950) is usually used. It includes 5 types: Asterad, Caryophyllad, Chenopodiad, Onagrad and Solanad. In each type, based on the specificity of the first divisions in the proembryo, the number of layers in it, the structure of the organs of the emerging embryo (these signs are not universal and in each case indicate only some features of embryogenesis) and a different number of variations is distinguished. That is, why they cannot be used for taxonomy and phylogeny. There is also a system of embryonomic types of embryo development proposed by SOUÈGES (1939), however, it is difficult to perceive and is hardly ever used at present (SHAMROV 2006). But this author proposed that in the course of evolution, the role of apical cell increased and the role of basal cell decreased. From these positions, the Caryophyllad-type of embryo development is the most specialised, since the basal cell does not participate in the construction of the embryo and is only part of the suspensor.

In the analysis of endosperm and embryo development systems, we consider our proposed classification of endosperm development types and the classification of JOHANSEN's (1950)

embryogenesis types. In both systems, division of the primary endosperm cell or zygote occurs transversely. There is evidence in the literature that the first division may be longitudinal or inclined or even not accompanied by the formation of a cell wall. Examples of similar endosperm development have been discussed above. We have also already mentioned special types of embryogenesis (Paeoniad-, Piperad- and Poad-types). Thus, as a result of the first division, many angiosperms have two cells (micropylar and chalazal in relation to the endosperm and apical and basal in relation to the embryo) (Fig. 6A). After this, the process of diversification begins.

The divisions are carried out in both cells (Cellular type of the endosperm), or at least in the micropylar cell where the nuclei arise (Helobial type of the endosperm). Formally, Asterad-, Caryophyllad-, Chenopodiad-, Onagrad- and Solanad-types are not identified after the stage of the bicellular proembryo. Existing modes of embryo development form clusters that differ in a complex of features. In Onagrad- and Asterad-types, as a result of division of apical (longitudinal) and basal (transverse) cells, a T-shaped cell tetrad is formed. In the Solanad-, Chenopodiad- and Caryophyllad-types, four cells arising during the second generation are linearly arranged. When analysing the contribution of derivatives of the apical and basal cells to the construction of organs of a mature embryo, the composition of the clusters changes. In Onagrad- and Solanad-types, the main part of the embryo is formed from derivatives of the apical cell, while hypophysis and suspensor arise from derivatives of the basal cell; in the Asterad- and Chenopodiad-types, both cells take more or less equal part in the organisation of the embryo; in this case, the cotyledons and shoot apex emerge from the apical cell and the hypocotyl, root apex and suspensor from the basal cell; in the Caryophyllad-type, the basic structures of the embryo are formed on the basis of the apical cell and the basal cell gives rise only to the suspensor. Consequently, **the 'types' of embryogenesis do not correspond to the types of development of the endosperm** but to a different status. We used both characteristics in distinguishing types of embryogenesis (the contribution of the apical and basal derivatives to the embryo construction; the mode of the divisions of the apical and basal cells and the shape of the tetrad) in characterising **subtypes** (the contribution of the derivatives of micropylar and chalazal cells to the construction of the endosperm) and **variations** (the mode of the divisions of micropylar and chalazal cells and tetrad form) of the **endosperm**.

Since such structures (haustoria and suspensor) appear in the forming seed and perform similar functions in the transport of metabolites, their presence also allows us to carry out a comparative analysis between the endosperm and embryo development systems. However, with this comparison, Helobial type is excluded from the types of endosperm, because after the stage of two cells in the latter, the nuclear divisions usually occur. In addition and as a rule, one variant of the haustorium–suspensor is comparable to the chalazal haustorium in the embryo. In the endosperm, both chalazal and micropylar (terminal) haustoria can form. Nevertheless, similarly to the selected subtypes in the cellular type of endosperm (according to the degree of participation of micropylar and chalazal cells in the construction of the endosperm), the Micropylar with chalazal haustorium subtype (the endosperm is formed due to the micropylar cell and the chalazal cell functions as a haustorium) is comparable to the Caryophyllad-type of embryogenesis (in the latter, the basal cell is part of the suspensor). Since the divisions in the micropylar cell of the endosperm occur in different directions, including obliquely, the shape of the tetrad is difficult to determine. Therefore, such a subtype of the endosperm is represented by only one variation – the *Nymphaea*-variation (Fig. 6C). The second subtype, Micropylar–chalazal without

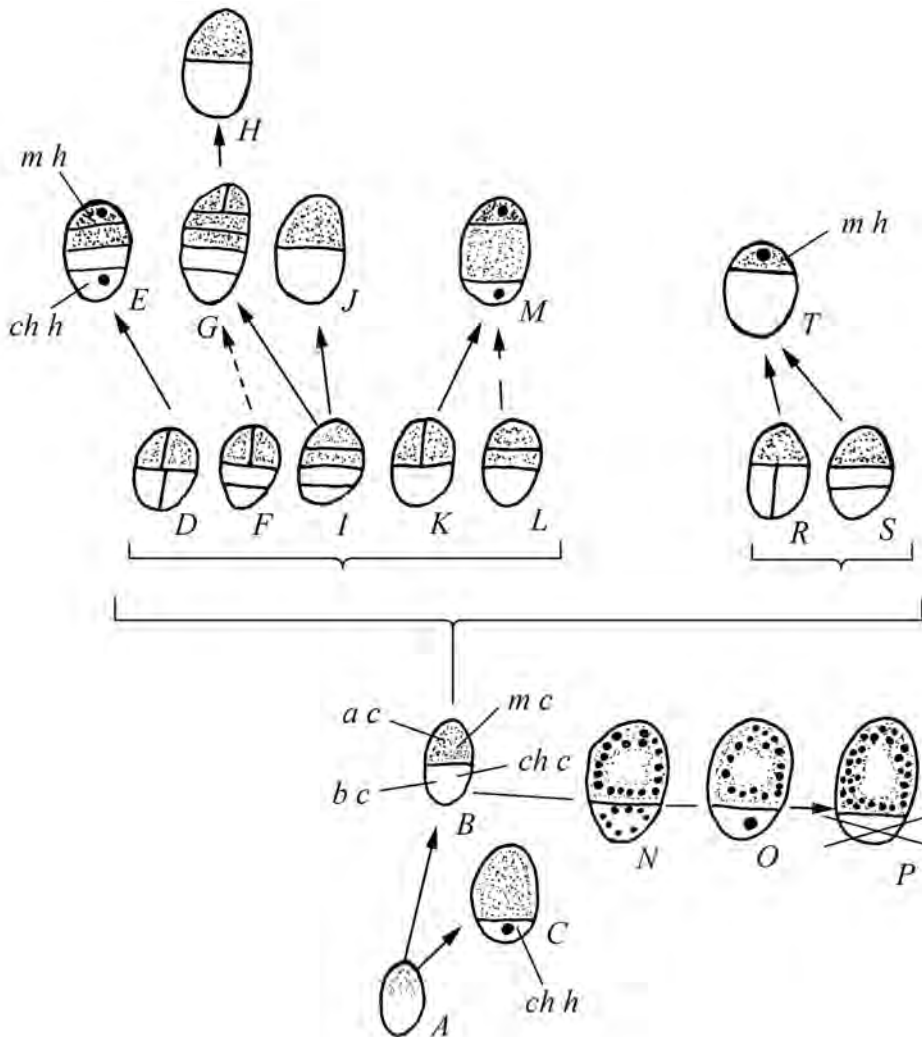


Figure 6. Scheme of possible interconnections between embryo and endosperm development in flowering plants (explanation in the text). A – initial cell of embryo (zygote) or endosperm (primary cell of endosperm); B – dyad of cells (apical and basal for embryo and micropylar and chalazal for endosperm); D, F, I, K, L, R and S – tetrads or triads of cells; C, E, H, J, M, T, N, O and P – contribution of apical and basal cells in embryo construction and micropylar and chalazal cells in endosperm formation; G – development stage of endosperm. *chc* – chalazal cell, *chh* – chalazal haustorium, *mc* – micropylar cell, *mh* – micropylar haustorium. Dots show the derivatives of the apical and micropylar cells, and blank – derivatives of the basal and chalazal cells. The successive stages of formation are indicated by arrows. Dotted arrows show possible ways of development.

haustoria subtype of the endosperm (both cells take almost equal part in the formation of the endosperm) can be compared with the Asterad- and Chenopodiad-types. Moreover, the presence of a single *Annona*-variation in the Micropylar-chalazal endosperm type without haustoria (the second division is transverse in both cells and a linear tetrad of cells forms) characterises only the Chenopodiad-type of embryogenesis (Fig. 6I, J). The representatives of Ceratophyllaceae with Asterad-type of embryogenesis have no haustoria, not only during the formation of the endosperm but also during the formation of the embryo (no suspensor) (SHAMROV & BATYGINA 1984). The endosperm in *Ceratophyllum* is represented by a linear tetrad after two generations (*Annona*-variation), longitudinal division in the uppermost cell occurs after the third generation

(Fig. 6G, H). And therefore, the endosperm becomes similar to the structure of the embryo of the Asterad-type (T-shaped tetrad of cells). Among plants with Asterad- and Chenopodiad-types of embryogenesis, there are those, which are characterised by a suspensor (Amaranthaceae, Asteraceae, Chenopodiaceae). Therefore, their structure and development of the embryo can be compared with Micropylar-chalazal with terminal haustoria subtype of cellular endosperm: a micropylar cell divides longitudinally and a chalazal cell transversely, which leads to the formation of a T-shaped tetrad of cells, *Phyteuma*-variation (as in Asterad-type) (Fig. 6F, E), second division in both cells is longitudinal with the formation of an isobilateral cell tetrad, *Scutellaria*-variation (in Chenopodiad-type, tetrad of cells is linear, but already at the stage of the octants, the apical part of the embryo becomes similar to the isobilateral tetrad) (Fig. 6D, E). The Micropylar subtype with terminal haustoria (the endosperm is formed from the lower derivatives of the micropylar cell and the chalazal cell, like the upper derivatives of the micropylar cell, forms terminal haustoria) is close to the Onagrad- and Solanad-types of embryogenesis. At the same time, *Prunella*-variation (the second longitudinal division occurs only in the micropylar cell, a T-shaped triad of cells is formed) is close to the Onagrad-type of embryogenesis (Fig. 6K, M) and *Callitriche*-variation (the second transverse division occurs in the micropylar cell, a linear triad of cells appears) to Solanad-type (Fig. 6L, M).

It should be noted that the Caryophyllad-type of embryogenesis (the apical cell forms embryo body and the basal cell is part of the suspensor) is comparable to the helobial endosperm (the micropylar cell arises endosperm proper, and chalazal one gives rise to chalazal haustoria (an uninuclear haustorium, *Limnocharis*-variation; a multinuclear haustorium, *Dianella*-variation; the chalazal cell is reduced during ontogenesis and phylogenesis, nuclear endosperm proper) (Fig. 6N–P). Besides, there are no models of embryogenesis, that are similar to the Chalazal with a micropylar haustorium subtype in the early stages: only the chalazal cell is transversely divided, resulting in a linear triad of cells, *Pedicularis*-variation; a longitudinal division in the chalazal cell and the triad of cells is inversely T-shaped, *Pentaphragma*-variation) (Fig. 6R–T). In this case, the endosperm body is formed only from derivatives of the chalazal cell. This also includes Chalazal without haustoria subtype. Examples of such modes of embryo development are not known.

Conclusion

Analysis of the embryo and endosperm development in flowering plants revealed a complex of characters that can be used for taxonomy and phylogeny. In a comparative analysis, the types of embryogenesis are most often used. As for the endosperm, the types of its development do not correspond to the 'types' of embryogenesis but to a different status. For the first time, this analysis includes the cellular mode of endosperm development, which some authors (DI FULVIO 1983; DI FULVIO & COCUCCI 1986) gave the status of a megatype of 5 types and 12 subtypes. However, the types and subtypes of these authors are not sufficiently substantiated, while literature data on the presence of different modes (types, forms, variations) of the endosperm are not used. Without resorting the use of the megatype category, the types of embryogenesis can be compared with the subtypes and variations of the cellular type of the endosperm, while both features (contribution of micropylar and chalazal cell derivatives to the construction of the endosperm; the character of the division of these cells and the shape of the tetrad) at the same time. Apparently, the possibilities of the helobial endosperm can also be taken into account with the presence of two subtypes and three variations.

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