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Evolution of sexual structures in higher plants (main types of meiosis)

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Abstract

A new conception of evolutionary development of sexual structures in *Magnoliophyta* is presented. This group has no gametophyte phase. Their gametes differentiate in the following pattern: somacyte — meiocyte — gametocyte — gamete.

Botanists consider that higher plants originated in the remote palaeozoic era from *Rhynophyta*. The latter in turn developed from *Chlorophyta* or *Phaenophyta*. But how to treat angiosperms having a very high degree of structural and sexual organization? Where should we look for their ancestor which formed the basis for the subsequent evolution of this group of higher plants? Takhtajan (1966) points out that flowering plants could not originate from *Gnetales*.

Among possible ancestores of *Magnoliophyta* from *Pinophyta*, there could be named only the majority of *Bennettitales* and some *Cycadeoidaee*. It is quite possible that *Bennettitales* and flowering plants are closely related as they originate from the same still unknown. In studying the phylogenetic relationship among higher plants the homology of the embryo sac of angiosperms with the gametophyte of gymnosperms represents a very important feature.

We agree with Maheshwari's (1950, p. 418) opinion that "It sems impossible to interpret the female gametophyte of angiosperms, with all its varied modes of development, in terms of archaegonium formation. As is known from our knowledge of the prothalli of pteridophytes and gymnosperms, archaegonia are initiated only in a cellular phase. In the angiosperms on the other hand, we are taken back to the 2-nucleate stage of the embryo sac as the point of origin of the archaegonium initials, which is pushing morphology into absurdity. It seems far more likely instead that the angiosperms have long passed the stage of archaegonia or that they never had them at any time in their fossil history".

I propose a new conception on the genesis of sexual structures in *Magnoliophyta*. That would permit us to outline the new way of treating the problem of the origin of this group. It is necessary to begin with the genesis of gametes which take part in the formation of the zygote or embryocyte. The process of sexual reproduction is the main link in the preservation of species and understanding of the evolution in *Magnoliophyta*.

Data on the formation of gametes and the sexual process especially, are used very broadly in phylogenetic considerations.

The formation of gametes and sexual process became possible due to meiosis — which involves reduction in the chromosom number and the transition from diploid to haploid condition. In the opposite case a successive doubling of chromosom number would occur which would result in the accumulation of a great quantity of DNA and destruction of the organism.

In evolution there appeared three types of meiosis:

1. *The zygote type*. In some *Algae* meiosis takes place immediately after fusion of the gametes, i.e. at the first division of zygote. Diplophase is very short and remains within the bounds of the life cycle of the zygote-cell only.
2. *The sporogenous type*. Among *Algae* and vascular plants meiosis is the final link in the ontogenesis of sporophytes. Meiosis ends by the formation of haploid spores which germinate and give rise to a new generation — gametophytes. The latter form gametes.
3. *The gametic type*. Among *Fucales* and flowering plants there are no spores and consequently no antithetic generations. The meiotic cycle is followed by reduction in chromosome number and the formation of gametocytes and gametes.

Out of the three existing types of meiosis in the evolution of plants the most important were two types: the sporogenous and the gametic one. The latter type somehow did not attract the attenion of scientists.

If we turn to data on embryology we shall find that the gametic type of meiosis is well pronounced in *Magnoliophyta*. We know that inside the anthers and nucellus there are some peculiar differentiated cells — meiocytes. They differ from other cells by a denser cytoplasm and larger size. Meiocytes undergo meiosis which results in the formation of a tetrad of haploid cells that we have named gametocytes. Three of them disintegrate and only one gametocyte functions as a sexual coenocytic cell where the divisions of nuclei are of the coenocytic or free-nuclear character.

The nuclear divisions are synchronous in the gametocyte, its further development proceeds on the basis of coenogenesis, consequently there is no cellular differentiation. At the mitosis in the gametocyte a binuclear coenocyte with well-defined polarity is formed. At the second mitosis which proceeds synchronously a four-nucleate coenocyte, and finally the eight-nucleate coenocyte are formed. In the widespread *Polygonum*-type a multinuclear coenocytic structure is formed which may be called a mature macrogametocyte that corresponds to the embryo-sac with 8 potential sexual nuclei.

So far we have considered the gametocyte as a coenocytic cell in which the number of nuclei equals 2^3. All 8 nuclei of the gametocyte representing the third generation are genetically closely related. All 8 nuclei can be considered as potential gametes of the coenocytic cell.

After the formation of potential gametes there follows reconstruction of the coenocytic free-nuclear structure into a specialized cellular structure. Consequently, in a mature macrogametocyte or embryo sac three well differentiated cellular groups appear: the micropylar one with an egg-cell and two synergids the chalazal one with three antipodal cells and a central binucleate cell.

The above mentioned groups are well distinguished morphologically and functionally. Out of the eigth potential sexual nuclei only one becomes the nucleus of the egg-cell, two nuclei of the central cell retain their own syngamic properties, being capable of conjugating between themselves and the sperm, while five nuclei lose their sexuality owing to their specialization. There are nuclei of two synergids and of three antipodals, they play a specific role in the general complex of the embryo sac — sexual elements providing for the normal course of double fertilization.

Irrespective of the embryo sac development type (mono-, bi- and tetrasporic) in all cases there is a coenocytic structure, characteristic of the gametocyte and appearing at different stages of the development of the latter (Table 1).

Table 1

Comparative embryological characterization of gymnosperms and angiosperms

	Ovule	Gametophyte	Archaegonium	Embryo sac	Fertilization	Proembryo
Gymnosperms	leaf origin	nuclear-cellular endosperm (n)	oospheres	absent	syngamy ♀×♂= embryo	free nuclear stage
Angiosperms	axial origin	absent	absent	8-nucleate coenocyte	double fertilization= embryo (2n) endosperm (3n)	cellular stage

As regards the genesis of male sexual elements we have the same picture. The meiocyte forms a tetrad of microgametocytes, becoming the initial cell of pollen grain. Gametogenesis here bears a more accelerated character than in the formation of female gametes. During the first division of the gametocyte nucleus the binuclear coenocyte appears. One of the nuclei, however, ceases to divide further, while the other continues. The first nucleus takes on the vegetative functions and the second one forms the sperms. The pollen grains as well as the embryo sac are very specialized structures, but with an earlier differentiation of gametes and a single auxiliary siphonogamic cell. Thus, from our point of view the source of gamete formation in flowering plants is the derivative of the meiocyte, i.e. the gametocyte. The formation of gametes proceeds within a single diploid life-cycle of the organism and is based on the gametic type of meiosis.

It becomes evident that in angiosperms there is no gametophyte as antithetic generation. Apparently it should be recognized that in higher plants there were different ways and sources of sexual elements formation in the process of evolution, each of them providing its own phylogenetic line of development. In one of these lines — angiosperms — gametogenesis proceeded on the basis of meiosis of the gametic type without the participation of the gametophyte type (ontogenesis). This line of development must be considered as agametophytic opposite to the other phylogenetic line — gametophytic line that gave rise to *Rhynophyta*. Naturally, the question arises whether in the vegetal world there still exist such types of plants in which gametogenesis is not connected with the gametophyte phase, but proceeds on the basis of gametocyte.

Among *Phaeophyta*, in *Fucales* there exist species only in diploid (sporophyte) phase, while the gametophyte phase is absent. Meiosis takes place during the formation of gametes. In *Fucus* the oogonia develop in conceptacles from one single initial cell. At first, it divides into an external covering and internal basal cells. The latter, owing to the division of cells adjacent to the initial cell, is submerged into a receptacle. The nucleus of the initial cell of the oogonium after meiotic division forms four nuclei. Then follows one mitotic division, which results in the formation of eight egg cells surrounded by a common cover. The mature cover bursts and the oogonia are pushed out from their conceptacles. Simultaneously, the spermatozoids are formed in the male conceptacles in the same way. Fertilization of egg cells takes place in water at the time of their emergence from the conceptacle. The fertilized egg cell attaches itself to the substrate and begins to divide. It should be noted that the embryogenesis of *Fucus* bears a great resemblance to the embryogenesis of angiosperms, it follows the same cellular regularities. Hence, the question arises: should we not search for the clue to the problem of the embryo sac origin in *Magnoliophyta* without taking into consideration the alternation of gametophyte and sporophyte phases?

In conclusion we affirm that:

Gametogenesis of *Magnoliophyta* has its own characteristic features. During the formation of male gametes, the meiocyte gives rise to a tetrad of initial cells of the microgametocyte. In the case of female gametes, out of four cells of the tetrad only one becomes a megagametocyte, while the other three degenerate. The formation of potential gametes proceeds on the basis of the coenocytic structure. Potential gametes differentiate in the mature megagametocyte into an egg cell and the central two-nucleate cell. The nuclei of synergids and of antipodes lose their sexual potentiality. Such functional reconstructions contribute to the process of double fertilization. *Magnoliophyta* have no gametophyte phase. The formation of gametes proceeds according to the scheme: somacyte — meiocyte — gametocyte — gamete. We may consider as quite probable that *Cormophyta* have inherited the gametic type of meiosis from *Thallophyta*. Among the first pioneers of dry land we can mention *Zostorophyllita*. They have been found in deposits of the upper Sylurian. The new fossil genus, *Cooksinia* is considered as the most ancient among higher plants. The *Cooksinia* gametophyte has not been found, therefore we can consider that there was on gametophyte phase in its ontogenesis; this phase is also lacking in certain brown algae.

The gametophyte type of meiosis is the most progressive one and as such it is found in angiosperms. The formation of gametes in tissues of diploid organisms and the presence of double fertilization in angiosperms may be considered as aromorphoses in the evolution of flowering plants.

On what basis was the evolution of the generative sphere founded in *Angiospermae*? Let us turn to the statement of the French botanist O. Linée. He considered that pioneers of land plants had an axial structure in the form of cauloid. Its apex had a maristematic zone and the basis was in the form of rhizoids. Cauloids gave phylloids. In the apical meristem there arose sexual elements. Such a very primitive plant in the apical zone of which there formed female and male gametes, could be the prototype of angiosperms the more so as the presence of apical meristem opened great possibilities for the formation of additional generative structures.

Table 1 shows the characteristic features of angiosperms and gymnosperms. It is difficult to speak of their homology. The histogenetic and embryological development is quite different and in angiosperms it is associated with the gametic type of meiois whereas in gymnosperms with the sporogenous.

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