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Modes of embryonization in the evolution of the ontogenesis of modular organisms

Alexander A. Notov

Summary: Specific characteristics of embryonization have been surveyed. The wide distribution of complex life cycles causes the diversity of ways and means of embryonization. Many types of life cycle transformations are related to the reduction of one or two generations. Embryonization is connected to deep transformations of the structure and biology of different development phases. The ultimate reduction level of bionts is attained due to open growth of modular organisms.

Keywords: embryonization, modular organization, ontogenesis, life cycle, evolution, theoretical biology

Embryonization is one of the main trends in ontogenesis transformation of evolution of different groups of living organisms, initializing progress in their structural and functional organization. (Schmalhausen 1938, 1968; Khokhryakov 1978, 1981). As some researchers (Jägersten 1972; Vagin 1979) suggested that life cycles of the 'metazoan' type occurred through progressive embryonization and integration of the 'protozoan' cycle, which aided the formation of the metazoan colony ontogenesis. Due to the increasing interest in evolutionary developmental biology (Vorob'eva 2006, 2010a, b) the analysis of the ways and means of embryonization gains a special importance.

Initially, the embryonization concept arose on the basis of zoological data (Zachvatkin 1949). This aspect has been well researched in various animal groups (Fedotov 1966; Polivanova 1979, 1982; Severtsov 1981; Tichomirova 1991; Ivanova-Kazas 1995, 1996; and others). Plant biologists became interested in researching this problem later. The main stages of embryonization in higher and lower plants were described by Khokhryakov (1973, 1978, 1981) who recognized the ways of vegetative embryonization and de-embryonization. In the present paper, I survey the main ways and means of embryonization on the basis of distinction between modular and unitary organisms as two fundamental types of their organization. This approach provides a clearer view of the specific characteristics of evolutionary transformation of ontogenesis and allows to find correlations between biological, structural, functional and ecological characteristics within various groups of living organisms (Notov 1999, 2005, 2008, 2011).

The appearance of the modular organization concept is connected to the implementation of the systematic approach to biological objects (Harper 1981; Tomlinson 1982; Shafranova 1990; Gatsuk 2008). The analysis of modular and unitary living organisms allows to uncover striking differences in their functioning, individual development and considerable specificity in the cybernetic aspect. These differences define the different statuses of modular and unitary organisms in ecosystems and the specifics of their evolutionary transformation (Marfenin 1993, 1999, 2002, 2008; Notov 1999, 2005).

The processes of embryonization are widely distributed among modular and unitary living organisms (Khokhryakov 1978, 1981; Vagin 1979; Severtsov 1981). However, the characteristics of reproductive systems and life cycle spectrums of modular organisms define the peculiarities of the processes connected to the embryonization of ontogenesis. Clarification of the embryonization process will allow a better understanding of the principles which guide the functioning of living organisms and find possible mechanisms of the occurrence and transformation of modular and unitary organization (Notov 2009, 2010). Open growth of modular organisms premises the unity of embryogenesis, morphogenesis, reproduction, regeneration as well as the diversity of life cycles and the wide distribution of reproductive strategies that incorporate various types of vegetative and asexual reproduction (Levin 1959, 1963; Lodkina 1969, 1983; Ivanova-Kazas 1977, 1996, 1997; Zhukova 1983; Batygina 2000; Batygina & Vasilyeva 2002; Isaeva 2010; Batygina 2011). Cyclical morphogenesis causes the wide distribution of life cycles which include alternating generations (development forms) (Notov 2010). In this case, the various growth and reproductive cycles occur and a full ontogenesis can be seen as the aggregate of individual ontogenesis of each specimen from different generations (bionts, development forms) of a given species. Only modular organisms show life cycles with the alternation of two or more generations, three nuclear phases and all the main forms of meiotic reduction occur (zygotic, gametic, sporous and somatic forms) (Petrov 1986; Belyakova et al. 2006).

Unlike modular organisms, the unitary forms have closed growth with definite limits of their embryogenesis. Their ontogenesis is more determinated and the epigenetic component plays a smaller role in the development process. Vegetative and asexual reproductions are not characteristic for them; they occur infrequently in taxa of lower organization levels. Complex life cycles with alternation of generations are virtually absent within unitary organisms.

The diversity of embryonization modi in modular organisms can be demonstrated by using the main ways of life cycle transformation as an example. When creating a system for categorizing development paths one can use formulas that characterize the main qualities of life cycles (Notov 2010). Such formulas may be supplemented with informations about the type of biont organization (generation) (Tab. 1).

Modular plants, fungi and animals demonstrate similar modes of life cycle transformation (Tab. 1). In many groups a loss of autonomy occurs as well as the reduction of bionts of various nuclear phases. Such loss supports the integration of individual ontogenesis of various generations.

During embryonization the generation bonds become stronger after an increase of the reduction level of the subjugated biont and substantial changes in its structure, biology and ecology. In some cases the reductive processes result in a considerable transformation of the modular organization (Tab. 1). Open growth systems that are characterized by simpler morphogenesis and decentralized regulation support the reaching of the ultimate level of biont reduction. Due to these characteristics the reduction of the subjugated generation to a microscopic coenoecium structure is possible, even with complex structural and functional body differentiations (for example, the female gametophyte in angiosperms).

Loss of autonomy in the development of one of the bionts occurs gradually. In some red algae *(Audouinella gynandra* (Rosenvinge) Garbary) it is optional. A diploid tetrasporophyte develops independently and in some cases it may develop on the gametophyte (Vinogradova 1977; Van den Hoek et al. 1995; Batygina et al. 2006). At the next stage the loss of autonomy becomes

Table 1. Some modes and types of embryonization based on complex life cycles of modular organisms. B – biont (generation, development stage): H haplobiont, D diplobiont, DC dicaryobiont; D_1, D_2 – different generations of the same nuclear phase; a comma is used when there is an isomorphic alternation of generations (bionts); > – domination of one of the generations; ( ) = bionts are connected; {} – the formula of the life cycle of a hypothetic ancestral taxon; *[ ]* – organization type: *M modular*, *U unitary*, *M’, M”, M’”* types of modular organization with various levels of transformation due to reduction; ⟶ – possible ways of life cycle transformations.

Taxa	Modes and types
	$B_1, B_2 \rightarrow B_1 > B_2 \rightarrow (B_1 > B_2) \rightarrow (B_1 > B_2')$
PLANTAE	**Phaeophyta** $\mathbf{D}[M], \mathbf{H}[M] \rightarrow \mathbf{D}[M] > \mathbf{H}[M] \rightarrow \mathbf{D}[M]$ *Dictyota* *Macrocystis* *Fucus* $\rightarrow \mathbf{H}[M] > \mathbf{D}[M]$ *Cutleria*
	Embryobionta $?\{\mathbf{D}[M], \mathbf{H}[M]\} \rightarrow \mathbf{D}[M] > \mathbf{H}[M] \rightarrow \mathbf{D}[M] > \mathbf{H}[M'] \rightarrow (\mathbf{D}[M] > \mathbf{H}[M'''])$?Rhyniophyta Tracheophyta (cryptogamic) Tracheophyta (seminal) $\rightarrow ?\{\mathbf{H}[M] > \mathbf{D}[M']\} \rightarrow (\mathbf{H}[M] > \mathbf{D}[M'''])$ Bryophyta
FUNGI	$\mathbf{D}[M], \mathbf{H}[M] \rightarrow (\mathbf{H}[M] > \mathbf{D}[M''])$ Chytridiomycetes Zygomycetes $\rightarrow \mathbf{D}[M'']$ Oomycetes $?\{\mathbf{H}[M] > \mathbf{DC}[M]\} \rightarrow (\mathbf{H}[M] > \mathbf{DC}\ [M'']) \rightarrow \mathbf{D}[M'']$ Ascomycetes *Saccharomyces* $\rightarrow (\mathbf{DC}[M] > \mathbf{H}[M]) \rightarrow \mathbf{DC}[M'']$ Basidiomycetes *Ustilago*
ANIMALIA	**Cnidaria** $\mathbf{D_1}[M] > \mathbf{D_2}[M] \rightarrow (\mathbf{D_1}[M] > \mathbf{D_2}[U]) \rightarrow \mathbf{D_1}[M]$ Coronata $\rightarrow (\mathbf{D_2}[U] > \mathbf{D_1}[M']) \rightarrow \mathbf{D_2}[U]$ *Bougainvillia* *Pelagia*
	$B_1, B_2, B_3 \rightarrow B_1 > B_2, B_3 \rightarrow (B_1 > B_2), B_3 \rightarrow (B_1 > B_2) > B_3$
PLANTAE	**Rhodophyta** $?\ \{\mathbf{H}[M] > \mathbf{D_1}[M'], \mathbf{D_2}[M]\} \rightarrow \mathbf{H}[M], \mathbf{D_2}[M]$ *Acrochaetum* $(\mathbf{H}[M] > \mathbf{D_1}[M'']), \mathbf{D_2}[M] \rightarrow (\mathbf{H}[M] > \mathbf{D_1}[M'']) > \mathbf{D_2}[M'] \rightarrow (\mathbf{H}[M] > \mathbf{D_2}[M'']) \rightarrow$ *Polysiphonia* *Nemalion* *Liagora* $\rightarrow (\mathbf{H}[M] > \mathbf{D_2}[M'''])$ *Rhodophysema* $\rightarrow (\mathbf{H}[M], \mathbf{D_2}[M] > \mathbf{D_1}[M']) \rightarrow (\mathbf{H}[M] > \mathbf{D_2}[M] > \mathbf{D_1}[M'])$ *Audouinella* *Batrachospermum*
FUNGI	**Basidiomycetes** $(\mathbf{DC_1}[M] > \mathbf{H}[M]), \mathbf{DC_2}[M'], \mathbf{DC_3}[M']$ *Puccinia*

obligatory. Initial stages of sporophyte development in some brown and red algae are connected to the gametophyte (Belyakova et al. 2006). In higher fungi the dicaryotic stage is formed on the gametophyte. The development of the medusoid stage of many colonial coelenterates begins with the polyploid generation (Naumov et al. 1987). The integration of ontogenesis of three different generations is possible. In the case of somatic reduction, the gametophyte develops on the tetrasporophyte and the carposporophyte on the gametophyte (species of the genera *Batrachospermum* Roth, *Lemanea* Bory de Saint-Vincent).

The loss of biont autonomy stipulates their reduction which in some cases leads to a complete disappearance of one of the bionts. Developmental cycles with reduced diplobionts occur in Rhodophyta and developmental cycles with reduced haplobionts are known in Phaeophyta (Tab. 1). In some red algae, the interpretation of life cycle is rather obscure due to an almost complete loss of the carposporophyte. Along with the traditional hypothesis about the transition of the carposporophyte to a parasitic life (Vinogradova 1977; Petrov 1986; Van den Hoek et al. 1995; Belyakova et al. 2006) it is suggested that this generation had never existed in red algae and their carpospores occur due to multiplication of zygotes (Perestenko 1985). Almost complete reduction of one of the generations can also be observed in some brown algae (Perestenko 1985; Petrov 1986; Belyakova et al. 2006).

Reduction takes place in generations showing different nuclear phases but only within higher taxonomical groups. A regressive transformation of the haplobiont occurs in complex life cycles. This mode is the main one in higher fungi and higher plants where the diploid phases or dicaryotic ones have an advantage in development. The ultimate stage of reduction of the haplobiont can be seen in Basidiomycota. Even in Ustilaginales, the peculiar dicaryobiontic life cycle occurs (Jackson 1944; Diyakov et al. 2005).

The reduction of one of the generations is the main trend of life cycle evolution in higher plants (Tab. 1). In Bryophyta, the sporophyte (diplobiont) is reduced, whereas in seed plants, the gametophyte (haplobiont) is nearly lost. The role of the embryonization is of special importance in higher plants, in which the sporophyte dominates. The reduction of the gametophyte is connected to various characteristics of reproductive biology. With the reduction of the gametophyte, the fertilization stops depending on the presence of drops of liquid water. In a next transformation step the male gametes lose their mobility and turn into sperm cells. The function of the gamete is transferred to the siphon cell of the male gametophyte and shifted into the pollen tube. There are substantial changes from the biomorphological point of view (Khokhryakov 1973, 1978, 1981). In seed plants, all the processes and stages of development that are characteristic for higher plants are connected ot the maternal organism. It should be noted that the functional and biological characteristics of the elements of the life cycle are substantially transformed. The functions of the spores that are typical for sporophytic plants (reproduction, dispersal) are not fulfilled (Lodkina 1969). In seed plants, these functions are taken over by the seed, which is a complex structure including the germ of the new sporophyte. The ultimate level of reduction of the gametophyte can be observed in flowering plants. Their gametophyte is transformed into a embryo sac with seven nuclei.

In some cases, embryonization processes lead to the emergence of secondarily simple life cycles based on more complex ones. Examples can be found among modular animals. The suppression in development of one of the diploid generations occurs in Cnidaria. In some members of this phylum, either the polyploid generation (*Bougainvillia* Lesson, *Campanularia* Lamarck), or the medusoid generation (Coronata) is reduced (Naumov et al. 1987). In the case of a complete reduction of the polyploid generation (*Pelagia* Péron et Lesueur belonging to the order Trachylida), the life cycle looses the development stage with modular organization. Secondary unitary forms emerge as a result of a complete loss of the polyploid generation (Tab. 1). In plants and fungi, diplobiontic, haplobiontic and dicaryobiontic cycles may arise on the basis of complex life cycles with alternating generations (Petrov 1986; Diyakov et al. 2005; and others). In some cases, these changes lead to a significant transformation of modular organization which is lost in stages of life cycles like carposporophyte (Rhodophyta), basidium (the diploid development phase in Basidiomycetes), sporogon (sporophyte of Bryophyta) and embryo sac (the gametophyte in Magnoliophyta).

In unitary organisms, the main modus of embryonization is related to the shift to viviparity, when the initial stages of the development of the new organisms are closely connected to the maternal organism. Viviparity in modular plants and animals arises on the basis of different types of asexual and vegetative reproduction (Batygina et al. 2006). The emergence of new organisms in seed plants may occur due to different types of gemmorhizogeny, embryoidogeny (Batygina & Vasilyeva 2002; Batygina 2011). Some analogues of viviparia can be found among algae (Petrov 1986).

Therefore, the wide distribution of complex life cycles in modular organisms causes the variety of ways and means of embryonization. Many types of cycle transformations are connected to the reduction of one or two generations. Embryonization is connected to significant changes in structure and biology of different development phases. The ultimate reduction level of bionts is caused by open growth systems of modular organisms that are characterized by a simpler morphogenesis and decentralized regulation.

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Address of the author:

Alexander A. Notov
Tver State University
Faculty of Biology, Dept. of Botany
Zhelyabova St. 33
170100 Tver
Russia
E-mail: anotov@mail.ru

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