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How did modular organisms appear? Functional and evolutionary aspects

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Summary: Factors promoting the occurrence of signs of a modular organization (MO) are considered. Modular structure (MS) and open growth (OG) (cyclic morphogenesis) allow covering the maximum surface area and high functioning with minimum volume. As a rule, these features are combined with a sessile mode of life. Usually, only one biont in the reproduction cycles has MO. It mostly carries out the plasticity function and is characterized by a longer life expectancy. When analyzing the origin of MO, it is necessary to conduct a frontal investigation of the diversity of living objects with MO and unitary organization (UO), organisms that combine the features of both types in varying degrees, and the structures of unitary organisms with traits of OG and MS. Living beings with signs of MO could come into existence as a result of aggregation, propagation processes (incomplete asexual reproduction) and differentiation of the elements responsible for growth. Apparently, MO formed independently in different kingdoms of living beings and large evolutionary groups. Further analysis of appearance and development pathways of MO in various taxa is necessary.

Keywords: theoretical biology, evolutionary biology, modular organisms, modular organization, unitary organization, modular structure, open growth, concept of modular organization, evolution, asexual reproduction, differentiation, aggregation, integrity of biological systems, ontogenesis

Scientists first became interested in the appearance of organisms with open growth (OG) (cyclic morphogenesis), which have the ability to repeatedly form main parts of their body, in the 19th century. To some extent, it was connected with the attempt to understand what should be considered an individual organism in plants and colonial animals (Braun 1853; Haeckel 1866; Spencer 1867; Perrier 1881; etc.). Reviews of these studies and continuing analyses of these issues were published at various periods (Beklemishev 1964; White 1979, 1984; Marfenin 1993; Gatsuk 2008b; etc.). The formation of the concept of modular organization (MO) promoted the synthesis of knowledge from various fields of biology and an increase of interest in this phenomenon (Tomlinson 1982; Marfenin 1993, 1999, 2002, 2016; Notov 1999, 2005, 2011; Gatsuk 2008b; etc.). The concept is based on the idea of two principally different types of organization of living beings. They are characterized by different models of morphogenesis and ontogenesis (Marfenin 1993, 1999; Notov 1999, 2005; Gatsuk 2008b). Modular organisms, in contrast to unitary organisms, repeatedly form their main structural elements = modules. This characteristic of ontogenesis defines their structural, functional and regulatory aspects as well as the principles of ensuring the safety of reproductive systems, ecological and evolutionary specifics (Marfenin 1993, 1999, 2002, 2016; Notov 1999, 2005, 2010, 2011, 2015a, 2016a, b; Barthelemy & Caraglio 2007). A non-centralized regulation of the integration in modular organisms also appears to be a special mechanism of self-adjustment of a biological system (Marfenin 2002, 2016). All of these aspects allow us to consider MO as a special model object for any area of biological research (Notov 2011).

MO occurs in many plants, fungi, in various animal groups and in some prokaryotic organisms (Notov 2011). The question of possible ways how modular organization could appear is a topical issue of modern evolutionary biology (Marfenin 1993; Notov 2001, 2016a, b; Lüttge 2012). Such analysis would allow us to understand the specifics of chief directions of evolution in various kingdoms of living beings and to reveal the characteristics of ecological adaptation in various types of organization.

Important generalizations about this issue have been made concerning colonial animals (Marfenin 1993). However, modern studies usually just state a hypothesis about the type of organization that was primary for some groups or all invertebrate animals (Boero et al. 1998; Dewel 2000; Makrushin 2013; Martynov 2013; etc.). The conditions, factors and mechanisms of the appearance of the MO phenomenon have actually never been discussed.

The search for new approaches to solve the problem of appearance of MO is a question of topical interest. In addition to typical modular and unitary organisms, there is a great variety of living objects that combine characteristics of UO and MO to a different extent (Notov 2001, 2011). When investigating the origination of MO, it is necessary to consider the whole diversity of its occurrence (Notov 2009, 2011). It is also important to reveal its functional causation and evolutionary meaning. Some results of this approach are discussed in this study.

Materials and methods

Principles of evolutionary diatropics (Tchaikovsky 1990) were used in the critical analysis of botanical, zoological and mycological studies. According to these principles studying the origin of any phenomenon presumes the uncovering of factors, methods and ways of its formation as well as the analysis of the results of the evolutionary process. If the phenomenon emerged independently in different groups, it is necessary to make a detailed comparison of all the methods, ways and results (Tchaikovsky 1990). The author analyzed the diversity of modular and unitary organisms that represent different kingdoms from the point of view of the MO concept (Tomlinson 1982; Marfenin 1993, 1999, 2016; Notov 1999, 2005, 2011; Gatsuk 2008b; etc.).

The main characteristics of MO as well as the specifics of their manifestations in living beings from different kingdoms were revealed (Notov 2001, 2005, 2009, 2011). A comparative structural and functional analysis of organisms and structures with MO attributes was made. Special attention was paid to unitary organisms with independent structures that have MS or OG. The diversity of life cycles of modular and unitary organisms was investigated (Notov 2010, 2013). Developmental stages during which MO manifests were also analyzed (Notov 2001, 2013). Their role in the life cycle of studied organisms was evaluated.

Correlations between attributes of MO and specifics of biology, functioning and eco-morphology have been revealed. The main directions of possible evolutionary transformations and possible modalities of changes in organizational types were established. The possible options of mutual transitions from one type to another were analyzed (Notov 2009). Possible ways of MO formation and mechanisms of progressive structural and functional differentiation of modular organisms are considered (Notov 2009, 2015b, 2016a, b). The author identifies directions of frontal analysis of the life diversity from the viewpoint of the evolutionary significance of the appearance and development of MO.

Results

Modular and unitary organisms represent the fundamental organizational types of living beings (Marfenin 1993, 1999; Notov 1999, 2005, 2011). However, alongside with typical modular and unitary organisms there are those with various combinations of MO and UO (Notov 2001, 2011). In addition, the main characteristics of MO, MS and OG or cyclical morphogenesis (Shafranova 1981, 1990; Marfenin 1993, 1999; Gatsuk 2008a, b; etc.) may manifest themselves in different ways. Each of these characteristics is a complicated attribute that represents a complex of mutually dependent and mutually connected qualities. Growth is not always connected with active morphogenesis. Growth and morphogenesis processes may be separated in time and in space (Belousov 1979, 1993). However, our beliefs about OG assume not only an increase in size, but also the constant formation of new structures (cyclic morphogenesis). This understanding of OG means that two main qualities characterize the modular organizational type, OG and MS. In this case, MS is a consequence of OG.

The levels of connections between considered characteristics, the levels of their manifestation and, consequently, the levels of MO expression may vary. For example, many representatives of the phylum Echinodermata have MS, but OG is not typical. Some crustaceous lichens don't manifest cyclic growth processes on a macro-morphological level. The main combinations of these characteristics in living organisms are following: 1) MS forms as a result of OG (typical MO); 2) OG without MS on the macro-morphological level; 3) MS without OG; 4) no OG or MS (UO). When evaluating the degree of manifestation of the modular organizational type, it is necessary to pay a lot of attention to OG, because it defines repeatability and cyclicality of processes and structures and correlates with a lot of other characteristics of MO (Notov 2001, 2005, 2011).

Organizational diversity of living beings increases rapidly due to various forms of manifestation of analyzed characteristics (OG and MS). They differ by: 1) level and scope of structures with attributes of MO; 2) duration of realization in ontogenesis; 3) degree of determinacy of expression; 4) degree of manifestation of characteristics. Some examples of described parameters are presented below.

1. Level and scope of structures. Attributes may be expressed on the level of the entire organism (MS in Echinodermata, OG in platelike algae); individual macro-structures (MS in arthropod extremities, bird feathers; OG in mammal nails, hair, horns, fish scales); only individual micro-structures (MS in neuron axons, certain chromatophores).

2. Duration of realization in ontogenesis. Characteristics may arise throughout ontogenesis or only on certain stages. For example, species from *Nocardia* (Actinomycetes) have a mycelium with MS and OG, which breaks down into individual fragments during the aging process (Kalakutskii & Agre 1977). During certain ontogenetic stages the endoparasitic crustacean *Thompsonia* goes through de-metamerisation (Dogiel et al. 1962). OG appears in the bronchial tree of mammalian embryos for a limited period of time.

3. Degree of determinacy of expression. Along with organisms and structures which have evident characteristics under any circumstances, there are those in which MS and OG appear only under certain developmental conditions (mycelia forms in surface cultures or yeast-like forms in deep cultures of fungi (Cherepanova 1981; Bilai 1989) and similar variants in Actinomycetes (Kalakutskii & Agre 1977)).

4. Degree of manifestation of characteristics. MS manifests in various degrees due to various levels of module development. Modules are weakly separated structurally and functionally in sponges (Spongia), some hornworts and liverworts as well as algae. Levels of integration of growth processes also differ (there are objects with diffuse meristematic activity and covert morphogenetic cycles as well as objects with clearly separated meristems and cycles). One of the criteria of a high level of MO development could be a significant level of morphological complexity of the body and a hierarchical differentiation of structural units.

Thus, many different combinations of MO and forms of its manifestation become evident in the process of analyzing the entirety of the diversity of living organisms. Living beings make up a huge continuum (Notov 2001, 2011). Typical unitary organisms, in which no characteristics of MO are fully and clearly expressed, are one extreme. Alternatively, typical modular organisms which fully show all the main characteristics of MO in the entire living object are located at the other end of the spectrum. In this case, MS is not a result of OG. Many correlations of specific attributes of ontogenesis with other peculiarities of biology, ecology, evolution and systematic organization are revealed (Marfenin 1999, 2002, 2016; Notov 2005, 2011, 2016a, b). Modular organisms are heterogeneous, if we take into account many aspects in the analysis of living beings (Notov 2011). They are rather diverse in terms of taxonomy and ecomorphology, and they represent various types of metabolism and structural organization. They differ significantly in the levels of morphological complexity and degree of integration.

How do we answer the question of the appearance of modular living beings? The author believes that we cannot limit ourselves only to studying various groups of typical modular organisms. It is necessary to make a frontal analysis of the diversity of living beings with MO and UO, organisms that combine characteristics of both types to varying degrees and some structures with OG and MS that are presented in unitary organisms.

The structural analysis of the functional causality of MO and possible mechanisms of evolutionary transformations of organizational types is of particular significance in finding ways of MO origination (Notov 2009). From the functional aspect, it is important to identify factors that promoted the formation of attributes of MO and the role of modular bionts in life cycles (Notov 2005, 2009, 2011). The evolutionary aspect assumes the consideration of various pathways of transformation of organizational types. The main tendencies that promoted the appearance of MO should be considered from those standpoints.

Functional aspect

Factors that ensure the appearance of signs of MO

Modular structure (MS). Some elements of MS may be found among unitary organisms. However, in case of UO, the formation of such elements is not connected with OG. In multicellular organisms, they are formed during embryogenesis as a result of multiple structure bookmarking or as a result of a very short morphogenesis stage with features of OG. Analysis of such elements of MS in unitary organisms allows us to identify the functional basis of their appearance.

The most widespread example of MS are branching structures. Branches allow covering the maximum surface area with minimum volume (Shafranova 1981, 1990; Aleev 1986). Dendritic and branching structures appear primarily in systems in which intensity of functioning mostly depends on the ratio between surface area and volume.

Within one taxonomic unit, the tendency toward branching out originated together with the increase of the organism's size and/or increase of organizational level. This tendency can be seen in the analysis of structures that carry out various functions. For example, some of the structures that developed branches were the ones that carry out the function of attaching to substrate. Among them are hooks and suction cups of Cestoda, flagella of trypanosomes or *Cryptobia* and algal rhizoids (Hausman et al. 2003). Branching forms of various supporting surfaces can be found: legs of copepods (Copepoda), bird feathers, some elements of radiolarian and foraminifer shells. Branching is often typical of structures that ensure various regulatory connections. Examples are the antennae of insects (night butterflies) and copepods, chromatophores, receptor extensions and neuron dendrites, macronuclei of the infusoria *Ophryodendron*, *Ephelota*, *Conchophthirus* and *Metaphrya* (Hausman et al. 2003). Branching structures are widespread in digestive and respiratory systems. For example, the digestive system of *Fasciola*, gills, trachea and lungs, the cardiovascular system. In many cases, the intensity of reproduction is also increased by branching processes (elements of the Cestoda reproductive system, gleba of the Gasteromycetes). Branching structures also appear in regulatory systems (osmoregulating pusules in Dinoflagellata).

MS may appear in the formation of several identical structures. Multiplicity of similar structures may often be observed in radial-type symmetry. In that case, it appears as a result of symmetry of the environment towards an organism or structures. Examples are representatives of Echinodermata, jellyfish tentacles and *Actinia*. Multiplicity of structures may be combined with their branching which increases the total covered surface area. In different groups, forms of branched tentacles and other structures can be found (sessile worms, infusoria). Multiplicity of typical structures is also characteristic of living organisms with an insufficiently high level of functional and structural body differentiation (metamerism in worms and some arthropods).

Open growth (OG). Some structures with the capacity for OG can be found among living beings with UO. They include hair, feathers, horns, rodent incisors, claws and nails of vertebrates, strobila of Cestoda. Often, these structures or their parts are functionally more ephemeral than other components of the organism's physiological structures. Functioning of such structures with OG is connected with the necessity of periodical full or partial renewal. OG is also typical of some structures in which growth is in agreement with isometric growth of the organism (gill covers, otic, fish scales, plates reptiles).

Modular structure and open growth (MS & OG). The combination of these two features is the most significant characteristic of living beings with MO. Organisms with MO have the above mentioned features at the level of the entire organism. The effectiveness of all life processes in such organisms depends significantly on the optimal balance between body surface area and its volume. Such dependency is observed primarily in adsotrophic nutrition, which assumes the ingestion of nutrients through the entire body surface (Aleev 1986). This correlation ensures a significant morphological segregation of the body. Such organisms interact with the environment by changing the intensity of form-building processes (Yurtsev 1986; Marfenin 2002). This type of interaction is a typical feature of systems with decentralized self-regulation (Marfenin 2002, 2016). To some extent, this option is connected with sessile (non-motile) lifestyle (Shafranova 1990). Only certain modular organisms have a mobile mode of life (for example syphonophores, *Cristatella mucedo*).

As the relationship between the organism and the environment evolutionary evolves, symmetric properties appear. A significant level of the internal environment differentiation affirms high organization of the unitary organism. In vertebrates, this environment assumes some feature of 'modular structure'. It is significantly 'branched' and morphologically 'divided' as a result of the specific structure of their respiratory and cardiovascular systems.

Life cycles of modular organisms

At least one stage in the life cycle of modular living beings has UO. Spores with no MS can be found even in the simplified cycles of Actinomycetes with modular mycelium. As a rule, MO is typical of one or rarely two stages of a life cycle (Perestenko 1972, 1985; Kamnev 1989; Notov 2010, 2013).

Generations (bionts) and other elements of the life cycle that have different types of organization also differ in their functional role, life span, size, movement abilities, level of differentiation and complexity of structure. Sometimes, they have different modes of nutrition. Stages with UO usually execute the dispersing, reproductive or attachment functions (Khokhryakov 1973, 1974, 1975, 1978, 1981a, b). During these stages, organisms are small in size, have a short life span and simple structure. They are usually able to move. Stages with MO are usually the main in the life cycle. Plasticity is its main function aimed at creating the basis for effective reproduction. This stage is characterized by larger sizes and longer life spans and usually by a sessile mode of life. In some groups of algae, life cycles with bionts have different organizational types and various degrees of MO expression (for example, Chlorophyta).

Lower organisms may have alternative types of individual development in which either unitary or modular objects are formed. They have been identified in some fungi (Cherepanova 1981; Bilai 1989) and Actinomycetes (Kalakutskii & Agre 1977). In anaerobic conditions, yeast-like forms are created. In aerobic conditions on the border between the two environments, a branched modular mycelium is formed. In this case, the border between environments acts as a factor of structural differentiation.

Evolutionary aspect

Transformation of organizational types

As a rule, the appearance of MO was connected with progressive evolution of various taxa. Transformation of UO into MO is the key tendency of groups in which MO is dominant. For example, the majority of multicellular representatives of the Chlorophyta are modular. MO formed in many groups for which adsotrophic nutrition and/or a sessile mode of life are typical. Transformation of MO into UO is very rare. Examples are 'secondarily singular' species of some coelenterates and bryozoans which occurred as a result of the colonial form reduction (Beklemishev 1964; Naumov et al. 1987). In some large taxa (Bryozoa, subclass Octocorallia), no 'primary singular' species were found and only colonial or rare 'secondarily singular' forms that formed due to reduction of colonial ones were found (Beklemishev 1964).

In some cases, only the simplification of MO with partial losses of its typical features occurred. Significant changes of the organizational type could also happen during the realization of the regressive tendency. For example, forms with traits of MO appeared as a result of the development of endoparasitism in some unitary invertebrate organisms. This was facilitated by the shift from the phagotrophic to adsotrophic mode of nutrition. Such changes have been noted among parasitic crustaceans. Representatives of *Sacculina* and *Dendrogaster* have bodies consisting of branching and growing threadlike structures which look like fungi hypha (Isaeva & Shukalyuk 2007). They are embedded in the host's tissues. At the same time, species of *Sacculina* are characterized by a rather long period of growth of branching. Some elements of MS can be identified in Gregarinida with branched bodies. In parasitic worms from the Cestoda group, the shift to adsotrophic nutrition was followed be the appearance of the capacity for OG (Dogiel et al. 1962).

In some higher plants, the shift from autotrophic to heterotrophic mode of nutrition facilitated significant simplification of the sporophyte MO, which is the main stage of their life cycle. At the same time, its vegetative body lost its primary shoot structure in representatives of Rafflesiaceae and Balanophoraceae. It was transformed into branching hypha-like structures. The typical shoot structure was also lost in Podostemaceae. Such reduction was due to the expansion into habitats in which plants undergo significant mechanical influences of rapid water currents. Significant reduction of the vegetative body could also happen in an aquatic mode of life as a result of intensification of vegetative reproduction. Species of Lemnaceae have lost primary MS (Ivanova 1973).

Interesting examples of partial transformation of MO can be found among gymnospermous plants. OG of their shoot system obtains unclear forms, and the module that is typical for the primary shoot is not reduplicated. Such transformation of the typical strategy of shoot formation in seed plants happened in *Welwitschia mirabilis*. It was also followed by deep transformations of the leaves of the primary shoot. As opposed to other seed plants with rather ephemerous leaves that have limited growth, the leaves of *Welwitschia mirabilis* are structures with OG. However, morphologically it is seen only in the unlimited increase of their length.

Characteristics of MO are usually lost in one of the bionts of the heteromorphic life cycles with changing generations. In different evolutionary groups of higher plants, the gametophyte and sporophyte were reduced. MO characteristics were completely lost in gametophytes of seed plants and especially flowering plants. In this case, the transformation of the organizational type was followed by the loss of the ability to exist independently, abrupt shortening of life expectancy and decrease in size, structure simplification and change in mode of nutrition (Notov 2012). Various examples of significant reduction of one of the generations that had MO can be found in red algae and fungi (Perestenko 1972, 1985; Vinogradova 1977; Zhukova 1983; Belyakova et al. 2006; Notov 2012; etc.). Such transformations make it more complicated to understand a life cycle and the structure of its elements.

Main tendencies that facilitated the formation of MO

MO is as widespread as UO. It appears in all kingdoms of living organisms, among representatives of various eco-morphological groups and types of structural organization (Notov 2011). MO was noted in unicellular and multicellular organisms, it is typical of some symbiotic associations which have a level of integration close to the level of an organism (lichens). Apparently, MO appeared independently in various groups, representatives of which had different levels of structural organization and differentiation (Notov 2009). When examining the factors and mechanisms of the formation of MO, it is reasonable to consider unicellular and multicellular organisms independently. In addition to significant differences in structural organization, they also have different types of genetic relationships. The full concurrence of the cellular level and organism level in unicellular living objects defines the different relationship between processes of growth, division and reproduction. In this case, the appearance of daughter organisms assumes the disappearance of the parental organism (Levushkin & Shilov 1994).

Reproduction of unicellular organisms usually happens only by means of cell (organism) fission. This type of reproduction is characteristic of most monobionts and some multinuclei metabionts. It appears that the tendency for the expression of MO features appeared in unicellular multinuclei metabionts. They have other types of reproduction (budding, fragmentation) alongside fission. These types of reproduction in modular unicellular organisms are more clearly separated than in unicellular unitary organisms. Growth of all unicellular organisms happens solely as a result of cell growth.

In multicellular organisms, the processes of growth, division and reproduction are realized both at the cellular level and the level of the entire organism. Cell division is already disconnected from organism reproduction (Levushkin & Shilov 1994). Reproduction happens due to the formation of special cells or cell complexes which are later separated from the parental organism. The parental organism doesn't disappear in this process. A type of asexual reproduction that assumes the fission of the maternal organism into two (or more) filial organisms (which is basically analogous to fission in unicellular organisms) is very rare in multicellular organisms. It appears in invertebrate organisms through longitudinal and transverse fissions which are connected by various transitions with budding (Ivanova-Kazas 1977). Growth happens at two different levels (at the cellular level and at the level of the organism). At the level of the organism, growth usually appears as a result of cell division. Increase in linear size of the organism is also mostly connected with cell division as opposed to the growth. The transformation of the developmental program of unicellular organisms that acquire MO is mostly connected with the processes of cell growth regulation and its relationship with division. Changes in the mechanisms of cell division regulation and cell differentiation become more important in multicellular organisms.

Appearance and development of MO could be to varying degrees connected with three evolutionary tendencies. They appeared independently at different structural levels and stages and promoted the appearance of living organisms that were more or less similar to modular organisms.

Formation of aggregations. Opinions about the integration of unicellular, and later on multicellular organisms, by means of aggregation were rather popular in the 19th century (Haeckel 1866; etc.). Formation of typical MO in this case is unlikely. However, in some cases and at certain stages, these processes could be important for the formation of living organisms with some characteristics of MO, primarily in groups with low organizational levels.

For example, this tendency appeared in the formation of plasmodia, pseudo-plasmodia and aggregate colonies of varying integration. As the level of their integration increased, the objects that were to some extent similar to modular living organisms appeared. Plasmodia of *Ceratomixa* resemble them as a result of MS. Branching aggregate colonies are also close to them. Integration of elements of such colonies may be carried out through mucus. In some cases, even cytoplasmic channels are formed. 'Mucus' colonies appeared in different groups of algae, bacteria and cyanobacteria and protozoa (*Spumillaria*, *Conochilus*) (Beklemishev 1964; Strelkov & Reshetnyak 1971). The developmental program of such colonies is weakly integrated. However, sometimes one can observe a determinate branching process, a certain localization of the fission process and the connection of its products through mucus (tree-like colonies of *Bacterium ramigerum* (Bacteriaceae), *Sphaerotilus* (Chlamydobacteriaceae), *Rivularia* (Cyanobacteria), *Licmophora* (Bacillariophyta), *Mischococcus confervicola* (Xanthophyta), *Hyalobryon*, *Dinobryon* (Chrysophyta)). When closer contacts in the aggregate are ensured by cytoplasmic connections, the number of elements in a colony could become fixed. The formation of the colony itself is coordinated and happens rather quickly in this case.

Formation of aggregates happens not only among unicellular, but also in multicellular organisms. For example, the aggregation of a multicellular mycobiont with algae (phycobiont) leads to the appearance of lichens which represent symbiotic associations. However, the level of integration of such associations is close to that of an organism. The level of structural complexity and coordination of processes of their morphogenesis may be rather high (Oksner 1974; Hammer 2000; Notov 2014; etc.).

Tendency for propagation. The belief that colonial organisms of invertebrates developed as a result of unfinished asexual reproduction appeared in the 19th century (Spencer 1867; Perrier 1881; etc.). Spencer assumed that when the appropriate conditions are met, the budding and fission processes don't go through to the end. Many filial organisms remain connected with the parental organism which creates the conditions for the formation of a colonial organism. In his opinion, a super-organism could appear as a result of progressive integration and growing specialization of multicellular individuals of the colony, e.g. colonial sea pens (Pennatularia) (Spencer 1867). These views have dominated zoological works for a long period of time (Beklemishev 1964; Ivanova-Kazas 1977; Aleev 1986; etc.). In some groups of colonial organisms, this path of MO formation is considered to be the most probable or the only one (Romanov 1997).

In multicellular animals and higher plants, a huge diversity of asexual (vegetative) reproduction with differing roles of disintegrative processes has been observed (Ivanova-Kazas 1977; Batygina 2014; etc.). To a large extent, it defines the popularity of the propagation hypothesis.

Differentiation of elements with morphogenetic activity. Researchers started to discuss this path of the formation of modular organization in relation to colonial organisms at later stages (Marfenin 1993). Detailed research on Hydrozoa demonstrated that their colonies are unified organisms. All parts of the colony (modules) are connected with each other. Their communication is enough to ensure system-wide processes. The analysis of forms and characteristics of the distribution of asexual reproduction in colonial organisms didn't provide reliable data in support of the propagation theory of MO formation (Marfenin 1993, 1999).

Discussion

It appears that the tendency for *aggregation* could lead to the formation of forms that are only more or less externally similar to modular organisms. Some characteristics of MS appear as a result of branching and inaequipermanence (unequal dates of appearance) of colony (aggregate) elements. However, connections between elements of such colonies are very weak and their developmental programs are characterized by low integration. The higher level of integration leads to fixation of the number of the elements and the higher integrity of the colonies' morphogenesis. This could define the preconditions for the appearance of multicellular organisms (Ivanov 1974; Ruiz-Trillo et al. 2007; Ruiz-Trillo & Nedelcu 2015). It led to a certain decentralization of the living organism (Ivanov 1974; Niklas & Newman 2013; Niklas 2014). Decentralization became one of the factors of transformation of unitary organisms into modular ones (Marfenin 2016).

The potential ability for localized growth that is characteristic of living objects with MO assumes certain autonomy of areas with growth activity. Such differentiation is more likely to appear on the basis of an already integrated developmental program, which is more characteristic of typical multicellular organisms. However, increased integration in colonies (aggregates) does not lead to the appearance of typical MO.

At the same time, aggregation could lead to the appearance of new types of objects with MO by means of integrating symbionts, one of which is a modular organism. That is how lichens appeared. As the connections between modular fungi and autotrophic phycobionts became stronger, the symbiosis became a significant factor in the progressive development of MO in lichens. The level of morphological differentiation of complexly branched thalli of lichens is higher than in fungi (Zmitrovich 2010; Notov 2014). Certain types of modules that didn't appear in fungi did appear in lichen evolution. For example, some lichens formed specialized lateral structures (phylloclades) on podetia (Notov 2014). Their appearance is connected with the functioning of the phycobiont. Thus, aggregations in the case of lichens became a factor of their structural diversity and development of MO in living objects that are not true organisms.

The tendency for *propagation* appeared in unicellular and multicellular organisms. Polyenergid unicellular organisms of varying structures could appear as a result of incomplete asexual reproduction. Propagation processes cannot be always clearly separated from differentiation. Drawing a line is especially difficult in microorganisms. For example, it seems that local growth in Hyphomicrobiales, Mycococcales and Mycoplasmae can happen both along with fission and independently of it (Krasilnikov et al. 1974).

Among ways of asexual reproduction of colonial organisms, variants of morphogenesis are connected with reproduction and OG. Examples are some types of fission and budding in invertebrates (Ivanova-Kazas 1977, 1995, 1996; Isaeva 2010). Budding mostly matches forms of differentiated growth, while asexual reproduction through fission in multicellular organisms is analogous to fission in unicellular organisms. Differences between fission and budding are most clearly seen in comparing longitudinal fission and budding on stolons (Ivanova-Kazas 1977). They differ in features of histogenesis as well as in the scale and direction of morphogenetic processes. Longitudinal fission is more similar to regeneration, because missing elements are being rebuilt. Local weakening of correlations can also be observed. The process of somatic embryogenesis appears during the budding on stolons. New zooids develop from histological elements, the formation of which is connected to deep local disintegration. The level of 'rejuvenation' of structures is higher (Ivanova-Kazas 1977). The occurrence of transformations of longitudinal fission into budding in some groups of ascidians (Ivanova-Kazas 1977) also points to a close connection between propagation and growth processes connected with the formation of new zooids-modules.

The specificity of typical MO is in the organic unity of embryogenesis, morphogenesis and processes of growth, reproduction and regeneration (Notov 2015a). Changes in the balance between reproductive and growth processes may lead to significant transformation of MO. Strengthening of the role of vegetative reproduction (overgrowth) may be connected with two opposite tendencies. In one case, deceleration of disintegrative processes is observed after formation of products of vegetative reproduction. In the other case, an intensification of disintegration appears. Deceleration of disintegration may promote the formation of MO or the appearance of MS without clear expression of OG. 'Secondarily' unitary objects may appear as a result of intensification of disintegrative processes. For example, intense vegetative reproduction in representatives of Lemnaceae led to significant transformations of MO. Quickly separating products of vegetative reproduction lost the primary shoot structure (Ivanova 1973) and became similar to unitary organisms.

Differentiation of elements with morphogenetic activity appeared in different groups of unicellular and multicellular organisms. The potential capacity for localized apical growth is typical of some microorganisms (Mycoccocus, Hyphomicrobiales, Mycobacteriales). The tendency for differentiation of growth areas played a special role in the evolution of algae with siphonal structures (Belyakova et al. 2006; Notov 2009, 2011; etc.).

Differentiation of growing elements appeared on a different structural basis in multicellular and unicellular organisms. In unicellular organisms, local growth appeared at certain parts of the cell. In multicellular organisms, body parts with stem cells that are capable of unlimited division were differentiated.

Differentiation of elements with the growth activity played an important role in the appearance and development of MO in many groups. At the latest stages, they ensured progressive development of MO independent from the initial way through which MO developed. Specialization of proliferate and meristematic zones occurred in different groups of multicellular organisms. Its main directions have been studied in detail in plants (Shafranova 1981). Evolutionary transformations of meristems after the attainment of high level of MO development were connected with the differentiation and specialization of various structures and programs of morphogenesis (Notov 2015b).

The character of further structural differentiation on the basis of MO was preconditioned by the features of the strategy of OG, which defines the specifics of the interrelation between the main organizational principles (Fig. 1) (Notov 2016a, b). OG that is expressed as cyclic morphogenesis is connected with multiple repeated realization of different and relatively autonomous morphogenetic programs. Appearance of these features is possible due to simplicity of morphogenesis. Taken together, the mentioned characteristics ensure wide distribution of vegetative and asexual reproduction, organic unity of embryogenesis, morphogenesis, processes of growth, reproduction and regeneration (Fig. 1) (Notov 2015a). The cyclic morphogenesis, high independence of developmental programs, relatively weak integration of modules lead to a rather weak integrity of structures, processes, ontogeny and the entire living system.

The polymerization reserve of structural elements that is characteristic of modular organisms becomes the basis for evolutionary transformations (Fig. 1). Their abundance, equivalence, low integrity, relative autonomy and structural simplicity create the conditions for integration by means of merging and combining elements (Notov 2016a, b). It is facilitated by a prominent ability to the fusion of structures and hierarchical differentiation of the body of modular organisms. Periodicity and cyclicity of integration processes and specifics of the interrelation between main organizational features lead to a pseudocyclic character of structural evolution of modular organisms (Notov 2016a, b). It is manifested in periodical 'assembling' of new structures of a higher level. They are externally similar to elements of lower levels that were combined during integration.

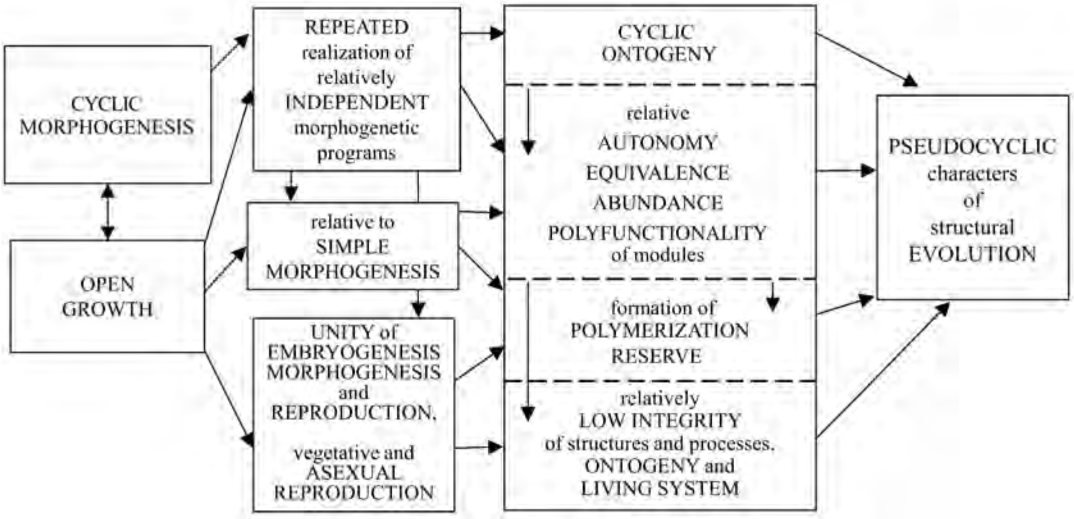

Figure 1. Character of interrelation between some features of modular organization.

Of course, appearance of MO played an important role in the evolution of invertebrates, plants and fungi (Khokhryakov 1973, 1975, 1981b; Marfenin 1993; Romanov 1997; Viskova 1999; Zhuravlev 1999; Notov 2009, 2011, 2014, 2015a, b, 2016a, b; Zmitrovich 2010; etc.). When analyzing the issue of the appearance of modular organisms, it is necessary to take into account some important features of the MO phenomenon.

Diversity of modular organisms is huge, their structural organization and level of MO expression differ significantly. At the same time, the level of structural and morphological complexity of modules doesn't always correspond with the level of integration and integrity of the modular organism. For example, zooids with complicated organization may have weak connections in colonies. Such colonies appeared among Ascidiae, Pyrosomida, Doliolida, Salpae (Beklemishev 1964; Naumov et al. 1987; Romanov 1997; Notov 2011, 2016a, b; etc.). It is widely considered to be highly possible that main models of colony structures, forms of branching in various clades appeared independently (Marfenin 1993; Romanov 1997; Viskova 1999; Zhuravlev 1999; Hageman 2003; McKinney & McGhee 2003; etc.). Asexual reproduction and differentiation of elements with morphogenetic activity should be accepted as key factors that could ensure MO origination. It is not always possible to clearly separate the two phenomena (see above) that could ensure the morphogenetic basis for MO. But the result is the same: repeated realization of the basic developmental program (Notov 2016a, b).

The possibility that appearance of MO happened several times and independently in various evolutionary groups and was carried out in different ways cannot be excluded. Formation and development of MO went through different stages. At the beginning, propagation could have played an important role (at least in colonial beings). At the stage of progressive development of MO, the processes of differentiation and specialization of elements of the form-building system which ensures OG began to play a key role. A shift in the balance between morphogenetic activity of OG systems and asexual (vegetative) reproduction combined with different intensities of desintegration could help promoting significant transformations of typical MO (for example, in higher plants). It seems that discussing ways of MO appearance in general is not completely accurate. In various kingdoms of living beings and in large evolutionary groups, the sources of modularity, factors and ways of the formation of morphogenetic bases of MO could be different. In the analysis of the evolution of large groups, all species of which already have obvious MO, the research goals will be different. In this case, it is worthwhile to clarify the features of the initial stage of MO development in the ancestral complex of the group.

Conclusion

The main attributes of MO are MS and OG. In typical modular organisms, MS is a consequence of OG. In this case, many correlations between features of their ontogenesis, biological, ecological, evolutionary traits and system organization can be observed. When analyzing the origin of MO, it is necessary to conduct a frontal investigation of the diversity of living objects with MO and UO, organisms that combine to varying degrees the features of both types and the structures of unitary organisms with traits of OG and MS.

Combining MS and OG allows objects to cover maximum surface area with minimum volume. As a rule, it correlates with a sessile way of life. In life cycles, MO is usually seen in only one of the bionts. It mostly executes the plasticity function and is characterized by a longer life span.

Living objects that are to varying degrees similar to modular organisms could appear as a result of aggregation, propagation and differentiation of elements with growth activity. It is likely that MO originated several times and independently in different taxa. It was brought about through various strategies. Formation and development of MO went through various stages in which the relative role of processes connected with the creation of a system of OG went through changes. At the initial stages, the propagations processes could have played a certain role (at least in colonial animals). Processes of differentiation and specialization of the system of form-building elements became a key at the stage of progressive development of MO.

A further analysis of MO origination and development in various taxa and kingdoms of living beings is necessary. A frontal analysis of the entire diversity of different organisms is very important. It will allow evaluation of the importance of different factors as well as means and ways of formation and transformation of MO in different groups.

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