

Pseudocyclic integration and evolution of modular invertebrates

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ABSTRACT: The Pseudocyclic (P) integration in modular organisms is determined by specifics in their morphogenesis, ontogeny and systemic features. P-transformations played an important role in the structural evolution of vascular plants. Modular animals are still insufficiently understood in this regard. The pseudocyclic similarities (PS) are found in different taxonomic groups of Coelenterata, Bryozoa, Urochordata. The probability of discovering of other PS increases owing to the hierarchical differentiation of the colony body and network character of structural evolution in different taxa of modular invertebrates. Further frontal analysis of the structural diversity of colonial invertebrates is important from the position of P concept. The results obtained in the analysis of vascular plants are useful in detail examination of the P-integration of modular invertebrates.
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KEY WORDS: colonial invertebrates, structural evolution, concept of modular organization, modular organisms, pseudocycles concept, evolutionary morphology, pseudocyclic transformation.

Псевдоциклическая интеграция и эволюция модульных беспозвоночных

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РЕЗЮМЕ: Псевдоциклическая (П) интеграция у модульных организмов обусловлена особенностями их морфогенеза, онтогенеза и системной спецификой. П-преобразования играли важную роль в структурной эволюции сосудистых растений. Модульные животные в этом отношении пока недостаточно изучены. Псевдоциклические сходства (ПС) отмечены в разных систематических группах Coelenterata, Bryozoa, Urochordata. Вероятность выявления других ПС повышается благодаря наличию иерархической дифференциации тела колоний и сетчатому характеру структурной эволюции в разных таксонах модульных беспозвоночных. Актуален фронтальный анализ структурного разнообразия колониальных беспозвоночных с позиции концепции псевдоциклов. При детальном исследовании П-интеграции у модульных беспозвоночных целесообразно использовать результаты, которые получены при анализе сосудистых растений.
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КЛЮЧЕВЫЕ СЛОВА: колониальные беспозвоночные, структурная эволюция, концепция модульной организации, модульный организм, концепция псевдоциклов, эволюционная морфология, псевдоциклическая трансформация.

Introduction

The modular organization is found in various kingdoms of living organisms. Most plants and fungi have a modular organization (Notov, 2011), but the animal kingdom it is represented only in invertebrates, with modular organisms of colonial Coelenterata, Bryozoa and Urochordata among them. Almost all modern concepts of the structural evolution of the vascular plants suggest directly or indirectly a wide distribution of P-integration (Meyen, 1973; Khokhryakov, 1981; Kuznetsova, 1986; Notov, 2016a, b; etc.). Modular invertebrates are still insufficiently understood in this respect. However, they have examples of pseudocyclic similarities (PS), which are also found in different taxonomic groups (Notov, 2016a, b; Timonin, 2001). Further estimation of the character of the relationships of P-transformations with the modular type of organization on the example of modular animals is an urgent task. The purpose of this study is to draw the attention of biologists to the examination of PS in colonial invertebrates.

P-transformations and modular organization

PS cannot be limited by any of the main types of similarities traditionally considered (Kuznetsova, 1986), as elements of the different hierarchical levels of organism structure are similar. These elements can be grouped into P-series, such as flower – simple inflorescence – complex inflorescence, or simple leaf – complex leaf – phyllomorphous branch – complex phylloclades. In such series, externally similar forms are repeated periodically on different structural bases. The P concept was used first in the analysis of morphological series of flowers and inflorescences, which contain repeated structures with a similar habitus related to one another as entirety and its part (see Kuznetsova, 1986). These series are, for example, formed by superficially similar flowers or simple and composite inflorescences. Almost immediately, the P-series has got an evolutionary interpretation (Gaussen, 1952). It was shown later the P concept can be used to analyze different structures of vascular plants (Kuznetsova, 1986).

The modular organisms are particularly interesting for the analysis of P-transformations (Notov, 2016a, b). The concept of the modular organization is based on the idea of two fundamentally different types of organization of living beings. They are characterized by different models of morphogenesis and ontogeny (Marfenin, 1999, 2008; Notov, 2005, Gattsuk, 2008b; etc.). Modular organisms, in contrast to unitary ones, have multiple development of modules, or major structural elements. This ontogenetic and systemic feature determines the specifics of their structure, function, and mechanisms of regulation, ecology and evolution (Marfenin, 2008; Notov, 2005, 2011; etc.).

Open growth, cyclic morphogenesis are connected with repeated realization of different relatively independent morphogenetic programs (Fig. 1). Manifestation of these properties is possible due to the simpler morphogenesis. Taken together, these characteristics allow vegetative and asexual reproduction, organic unity of embryogeny, morphogenesis, growth, reproductive, and regeneration processes (Fig. 1).

The polymerization fund (bank) of structural elements typical for modular organisms is a basis for evolutionary transformations (Fig. 1). Their abundance, equivalence, low integrity, relative autonomy, and structural simplicity serve as a background the integration of elements). The realization of the integration processes in modular organisms is facilitated by a prominent ability to fusion of their structures. It is very common in plants, animals, and fungi (see Notov, 2016a). The fusion of structures is facilitated by open growth, constant meristemic and morphogenetic activity. The analysis of extant and extinct taxa confirms a considerable role of fusion in the development of structural diversity in modular invertebrates (Beklemishev, 1950; Naumov et al., 1987; Viskova, 1999; etc.). Periodicity and cyclicity of structural aggregation are key attributes of morphological evolution. They provide the formation of mono-, meta-, and coenometabionts, which represent the ma-

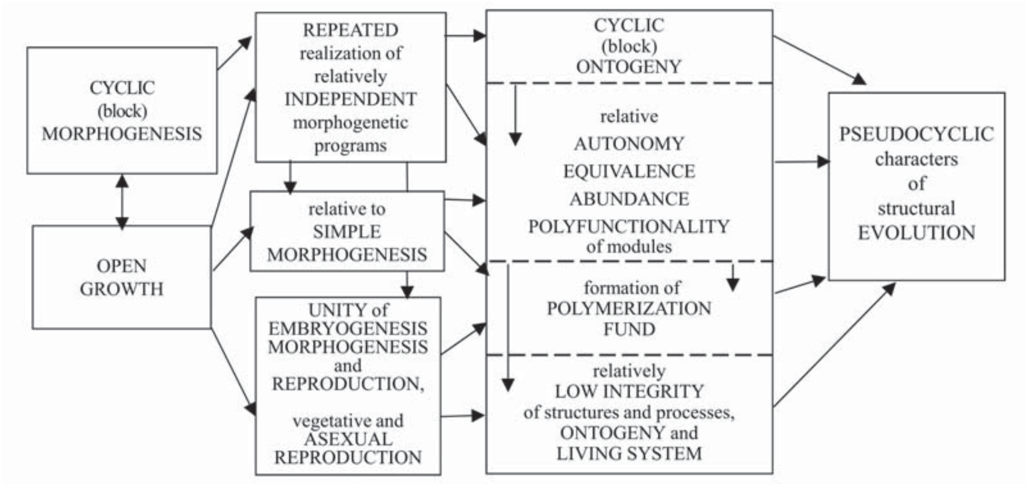

Fig. 1. Character of interrelation between some features of modular organization.
Рис. 1. Характер взаимосвязи некоторых особенностей модульной организации.

jor levels of functional organization of organism biosystems. The coenometabiont level is associated solely with the modular organization. In addition to this mainstream pathway, modular biosystems realize “intermediate” cycles of integration, resulting in a next qualitative increase in complexity of the morphofunctional organization (Khokhryakov, 1981; Notov, 2016a). P-transformations can occur in the cycles of any level, but they are mostly associated with the “subdominant” levels.

Searching variants of P-integration in modular invertebrates

The probability of appearance of P-integration increases owing to the hierarchical differentiation of the body of the colony in different groups of modular invertebrates (Viskova, 1999; Hageman, 2003; Sánchez, 2004; etc.). Unfortunately, from the morphological point of view, it is not yet studied sufficiently enough. Studying colonies, zooids and cormidia, sometimes general shape of the colony are usually analyzed (Beklemishev, 1950; Hageman, 2003; etc.). When describing branching, correlations between the main parameters, which reflect the proportionality of the colony structure, are usually found (Sánchez, 2004; Marfenin, 2008; etc.). A detailed analysis of the structure and morphogenesis is carried out very rarely (Marfenin, Kosevich, 2004; Kosevich, 2012; etc.). All this has not yet permitted researchers to develop a system of structural units of the colonies, one that would be similar to the system established for seed plants (Gattsuk, 2008a). Such a system would make it possible to study the structure and modes of transformation of units from each level, which would facilitate the identification of the PS.

When conducting detailed examination of the P-integration in modular invertebrates, it is expedient to use the results obtained in the analysis of vascular plants. The study of P-transformations in colonial animals is complicated by the absence (unlike in higher plants) of a single plan of structural organization of the elementary module and structural units of the colonial organism and by different degrees of development of module organization. The processes of separation of the vegetative and generative spheres within the general body of the organism-colony in animals were manifested less prominently than in plants. However, the structures and types of architecture found in plants have certain analogues in colonial animals. For instance, corals show certain architectural models described for tropical trees (Hallé et al., 1978; Dauget, 1991). The structure of inflorescences of angiosperms is compatible with variants of branching in colonial hydroid polyps. There are polythelic and monothelic types (Timonin, 2001), whereas the series of their transformations (Marfenin, Kosevich, 2004; Kosevich, 2012) can be compared with P-series of inflorescences. All this facilitates a search for similar P-transformations. As in higher plants, they are associated with different structural levels. PS found in animals are usually associated with structural elements (Notov, 2016a, b). The colonial level is studied clearly insufficiently.

Colonial level

Some equivalents of large-scale P-integration, associated with transformation of morphofunctional organization listed above for plants, in colonial animals, could be connected with the development of intergrated «monolith» and compound colonies. Such colonies are described in some corals, ascidians, and bryozoans (Dauget, 1991; Romanov, 1997; Viskova, 1999). Compound colonies are composed of subcolonies of a certain structure (Viskova, 1999).

The integration of different elements resulting in the development of colonies, which are externally and functionally similar to singular forms, is recorded in all large groups of modular animals (Beklemishev, 1950; Naumov et al., 1987; Romanov, 1997; etc.). For instance, bryozoans form colonies, like *Cristatella* Cuvier, due to a complete fusion of cystids. This led to shared locomotor muscles and nervous system, and the colony can reproduce by transverse subdivision (Beklemishev, 1950). Bryozoans also have compound colonies composed of several subcolonies (Viskova, 1999).

The formation of superficially "monolith" colonies of f ascidian can be represented as two P-series (Notov, 2016a). At the end of the first period, massive colonies were formed from zooids, while the second terminated with the cormidial colony (Romanov, 1997). The beginning of the next pseudocycle can also be revealed. In *Sycozoa mirabilis* (Oka), the integration of cloacal cavities of cormidia led to the formation of a single commoncolonial cloacal cavity. The transverse channels became "dissolved" in the central common cloacal cavity (Romanov, 1997).

Versions of integrations of zooids in "monolith" colonies are to some extent similar to the formation of pseudanthia in plants. For instance, the fusion of zooids in brain corals (Leptoria, Diploria, and Platygyra) led to the development of mouth openings surrounded by two rows of tentacles and a shared gastric cavity. The borders between zooids disappear and the colony becomes similar to a single organism ("secondarily singular" forms) (Naumov et al., 1987). In some cases, it resulted in the development of "secondarily singular" forms. Similar transformations are recognized in bryozoans, corals, and tunicates (Beklemishev, 1950; Naumov et al., 1987; Romanov, 1997; Viskova, 1999; Sánchez, 2002; Hageman, 2003; etc.).

Structural elements of colony

In hydroids, the integration processes led to the transformation of the shoot morphogenesis and development of monopodial colonies and terminal growth zones (Marfenin, 1993; Marfenin, Kosevich, 2004; Kosevich, 2012). A certain similarity of the transformation of the structural body organization in plants and colonial animals is revealed from the analysis of lateral "appendicular" and lamellar structures. They are characteristic, for instance, of sea pens (Pennatulacea). Similar to macrophyll elements, zooids were fused at their bases to form broad frondlike structures (Naumov et al., 1987). In gorgonians, the fusion of branches led to the formation of fanlike plates (Naumov et al., 1987; Sánchez, 2004). Lamellar structures are also found in bryozoans (Hageman, 2003).

The integration cycles of lower levels were associated with the development of "multi-individual organs" (Beklemishev, 1950) and "compound" colonial shared structures (systems). "Fronds" of species of *Aglaophenia* Lamouroux (Thecophora) representing a specialized cormidium can be interpreted as "multiindividual organs". This cormidium is composed of a series of feeding zooids, each enclosed in the hydrotheca and surrounded by three protective zooids. Within a basket, there are underdeveloped individuals of the medusoid generation (Naumov et al., 1987). These structures are superficially similar to pseudanthia of angiosperms. In some hydrocorals, the central gastrozoid with a large mouth is surrounded by mouthless dactylozooids resembling tentacles. The whole group is structurally and functionally similar to a single zooid. The cyanthium of the genus *Euphorbia* L. (Timonin, 2001) is organized in a similar way. Its central female flower is surrounded by monochasia of single-stamen male flowers. Original compact groups of zooids are found in hydroids of the order Chondrophorida. Their structure is similar to the model of an individual inflorescence of *Petagnia saniculifolia* Guss., which is composed of a central female flower and small male flowers fused with its ovary (Timonin, 2001). The polysiphonal stems in hydroids of the genus *Eudendrium* Ehrenberg, which are produced by the fusion of the axial elements of the colony, can be interpreted as "compound" colonial structures (Naumov et al., 1987).

Research perspectives

Numerous analogues of structural transformations in colonial invertebrates and plants suggest that a specialized analysis will confirm an even greater similarity of P-integration in different groups of modular organisms. Most authors pointed out independent origin of the main types of colonies and types of branching in many groups and clades of colonial invertebrates (Romanov, 1997; Viskova, 1999; Hageman, 2003; Marfenin, Kosevich, 2004; etc.). The network character of structural evolution suggests an even more considerable role of P-transformations in modular animals compared to the current thoughts. The frontal analysis of PS in different groups and taxa of modular animals is associated with the development of the concept of architectural models (Hallé et al., 1978; Dauget, 1991). There is not yet a system of structural units for colonial animals similar to that used for seed plants (Gattsuk, 2008a), but such a system would have facilitated the study of the modes of transformation of units at each hierarchical level. There is some progress of this kind in bryozoan studies, as cormidia and subcolonies have been recognized in bryozoans (Viskova, 1999). It is also necessary to involve a detailed comparative analysis of integration processes in modular and unitary animals.

Conclusions

P-integration wide distribution in the evolution of modular organisms was possible because of their morphogenesis, ontogeny, and systemic specifics. P-transformations happened in different taxonomic groups of Coelenterata, Bryozoa, Urochordata. Further development of theoretical zoology and evolutionary biology could be promoted by a frontal analysis of the structural diversity of modular invertebrates from the perspective of the P concept.

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