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Modular organization – a model for biological research

Alexander A. Notov

Summary: Different aspects of the diversity of living objects with a modular organization were studied. Clarification of the general and specific features of different taxa of biological groups of organisms with modular organization must be based on detailed studies of morphogenesis and ontogenesis. Comparison of modular and unitary objects allows to reveal not only the specific features, but also numerous equivalents. Such equivalents reflect common organizational principles and tendencies of transformation of living systems.

Keywords: modular organization, biological research, organizational principles, theoretical biology

Biology is a complex scientific discipline closely connected with various directions of research, system analysis and the cybernetic approach (Schmalhausen 1968). The concept of modular organization helped to unite the knowledge from various biological disciplines and to establish new issues of a general biological theme (Lodkina 1983; Shafranova 1990; Kuznetsova 1992, 1995; Marfenin, 1999; Notov 1999, 2005a). Recently, there has been a rise of interest in research of biological systematics and integrity of living organisms (Marfenin 2002; Vorobyeva 2006). It has been conclusively shown that modular organization is an interesting model in cybernetic studies. Non-centralized self-regulation of the integrity of colonial organisms poses a special mechanism of self-regulation of a biological system (Marfenin 2002). Results of such studies in this direction are interesting for neuroinformatics and for further development of the neural networks theory (Marfenin 2002). Modular organisms may be an interesting object for other fields of general biological and system studies.

Separation of organisms into 'modular' and 'unitary' reflects considerable differences in ontogenesis, structural and functional organization (Lodkina 1983; Shafranova 1990; Kusnetzova 1992, 1995; Marfenin 1999; Notov 1999). From the position of the modular organization concept it is possible to clearly emphasize and underline the specificity of the object in any direction of biological study. However, in addition to typical representatives of modular and unitary organizations, which have features of one type completely and clearly visible, there is also a wide variety of living objects that combine, to various extent, features of other organization types (Notov 1997, 1999, 2001; Khokhryakov 1997). Modular and unitary organizations are like two large centers in a huge continuum of living organisms. In the peripheral areas of this continuum are living objects that combine, at different levels, various features and characteristics of modular and unitary organization (Notov 2001). Typical modular organization assumes a rather full manifestation of features such as modular structure and open growth (cyclical morphogenesis) on the entire modular object. Here it is important that the modular structure is a result of open growth. In that case, there are numerous correlations with characteristics of ontogenesis and other important biological characteristics (Marfenin 1999; Notov 1999). Open growth should be given a lot of attention in the analysis of organization types that are close to modular organization, even if it doesn't lead to a modular structure on

Table 1. Characteristics of distribution of modular organization in various kingdoms of living organisms. We used a system from synoptic Russian literature (Fedorov & Takhtajan 1974–1982; Sokolov 1987–1989). M – modular, U – unitary organization type; M’, M” – presence of individual features of modular organization that are manifested clearly for M’ and less clearly manifested for M”.

Regnum	Taxa	
PROCARYOTA (U>M)	Cyanobacteria (U=M) Actynomycetes (M>U)	
FUNGI (M>U)	Divisio Myxomycota (U>M”) Divisio Mycota **Lower fungi** (M>U) Classis Chytridiomycetes (U, M’>M) Classis Oomycetes (M, M’>U) Classis **Zygomycetes** (M>U) Classis Trichomycetes (U, M’)	Divisio Mycota **Higher fungi** (M>U) Classis **Ascomycetes** (M>U) Classis **Basidiomycetes** (M>U)
	Lichenes (M>U)	
PLANTAE (M>U)	**Lower plants** (U>M) Divisio Pyrrophyta (U>M’) Divisio Chrysophyta (U>M’) Divisio Bacillariophyta (U) Divisio **Phaeophyta** (M>U) Divisio **Rhodophyta** (M>U) Divisio Xanthophyta (U) Divisio Euglenophyta (U) Divisio Chlorophyta (U=M) Divisio **Charophyta** (M)	**Higher plants** (M) Divisio **Bryophyta** (M>M’) Divisio **Rhyniophyta** (M) Divisio **Zosterophyllophyta** (M) Divisio **Psilotophyta** (M) Divisio **Lycopodiophyta** (M) Divisio **Equisetophyta** (M) Divisio **Polypodiophyta** (M) Divisio **Pinophyta** (M) Divisio **Magnoliophyta**(M>M’)
ANIMALIA (U>M)	**Invertebrate** (U>M) Subkingdom Protozoa Phylum Sarcomastigophora (U) Phylum Sporozoa (U) Phylum Cnidosporidia (U) Phylum Microsporidia (U) Phylum Infusoria (Ciliophora) (U>M) Peritricha, Suctoria (U=M) Subkingdom Metazoa Phylum Placozoa (U) Phylum Porifera (Spongia) (U=M’) *Radiata* Phylum Coelenterata (M>U) Classis **Hydrozoa** (M>U) Classis Scyphozoa (U) Classis **Anthozoa** (M>U) Phylum Ctenophora (U) Phylum Mesozoa (U) *Bilateria* Phylum Plathelmintes (U) Classis Cestoda (M”) Phylum Nemathelmintes (U>M”) Classis Kamptozoa (M”) Phylum Nemertini (U) Phylum Annelida (U) Phylum Tentaculata (U>M”) Classis Phoronoidea (U) Classis **Bryozoa** (M>U) Classis Brachipoda (U) Phylum Mollusca (U) Phylum Echinodermata (U) Phylum Pogonophora (U) Phylum Chaetognatha (U) Phylum Arthropoda (U) Phylum Hemichordata (U=M)	Subkingdom Metazoa Phylum Chordata (U>M’) Subphylum Tunicata Appendicularia (U) **Ascidiae** (U=M’) Pyrosomida (U=M”) Doliolida (U, M”) Salpae (U, M”) **Vertebrate** (U) Subphylum Acrania (U) Subphylum Vertebrata (Craniata) (U)

the macro-morphological level. Analysis from the position of modular organization of various living organisms allows to understand their organizational characteristics more fully and deeply.

Modular organization and its close versions can not only bee seen in various taxa of living organisms, but also in various biological groups. This allows to select modular objects for studies on any general biological issue.

The goal of this article is to explore the characteristics of the modular objects' distribution in various taxonomical and biological groups. The authors analyze the following aspects: taxonomy, biochemistry, ecomorphology, structure and systematics. We intend to evaluate the future of using modular organization as a model in structural, morphogenetical, ontogenetical, general biological and systematical studies.

Diversity aspects of modular living organisms

Taxonomical diversity

The results of a preliminary analysis of characteristics of distribution of modular organization in large taxa of living organisms are shown in Table 1. We used the system described in the six-volume edition of 'Plant Life' (Fedorov & Takhtajan 1974–1982) and the seven-volume edition of 'Animal life' (Sokolov 1983–1989). For prokaryotes, which classification is extremely debatable, and which vast majority of representatives have unitary organization, only names of taxa with features of a modular organization are given. We used nominal separation of fungi and plants into lower-level and higher-level, and animals into invertebrates and vertebrates. This was done to establish the dependence of the occurrence frequency on the level of group organization that is the most integral characteristic.

An analysis of Table 1 allows us to conclude that: 1) modular and unitary organizations can be found in all kingdoms of the organic world system; 2) modular organization is most widely spread among mushrooms and plants; 3) there are no virtually 'typical' unitary forms among higher plants; 4) typical unitary organisms prevail among the vertebrates; features of modular organization can be noted only in some tunicates; 5) 'higher' taxa are characterized by a clear prevalence of one organizational type. Some higher plants have secondarily lost a typical modular structure. Representatives of Lemnaceae are among them. A considerable transformation of the vegetative sphere structure in some groups occurred due to a parasitic lifestyle (Rafflesiaceae, Balanophoraceae) or due to growth under conditions of strong mechanical waterflow impact (Podostemaceae). However, in general these changes led to only a simplification of the plants' systems without any changes in the organizational type.

A taxonomical analysis of living objects with a modular organization that considers current perceptions of the macrosystem of the organic world is of interest at this time (Alimov 2000; Cavalier-Smith 2002, 2003; Sidorova 2003; Belyakova et al. 2006; Maddison & Schulz 2007; Margulis & Chapman 2009). Objects with features of modular organization can be found in more if not all kingdoms (Tabs 2, 3).

Types of metabolism

Combining the most important characteristics of the energy and biosynthesis we obtain eight main types of metabolism that occur in nature (Tchaikovsky 1990). Modular organization

Table 2. Characteristics of distribution of modular organization in various kingdoms of living organisms (system of Margulis & Chapman (2009)). Labels are the same as in Table 1.

Kingdom	Subkingdom	Divisio (Phylum)	U/M
PROCARYOTAE	Archaeabacteria	Euryarchaeota [B–1]	U
		Crenarchaeota [B–2]	U
	Eubacteria	Proteobacteria [B–3]	U
		Spirochaetae [B–4]	U
		Saprospirae [B–5]	U
		Cyanobacteria [B–6]	U=M
		Chloroflexa [B–7]	U
		Chlorobia [B–8]	U
		Aphragmabacteria [B–9]	U
		Endospora [B–10]	U
		Pirellulae [B–11]	U
		Actinobacteria [B–12]	M>U
		Deinococci [B–13]	U
		Thermotogae [B–14]	U
PROTOCTISTA	Amitochondria	Archaeprotista [Pr–1]	U
	Amoebamorpha	Rhizopoda [Pr–2]	U
		Granuloreticulosa (Foraminifera) [Pr–3]	U
		Xenophyophora [Pr–4]	U
	Alveolata	Dinomastigota [Pr–5]	U
		Ciliophora [Pr–6]	U
		Apicomplexa [Pr–7]	U
	Heterokonta	Bicosoecida [Pr–8]	U
		Jakobida [Pr–9]	U
		Proteromonadida [Pr–10]	U
		Kinetoplastida [Pr–11]	U
		Euglenida [Pr–12]	U
		Hemimastigota [Pr–13]	U
		Hyphochytriomycota [Pr–14]	U, M”
		Chrysomonada [Pr–15]	U
		Xanthophyta [Pr–16]	U
		Phaeophyta [Pr–17]	M>U
		Bacillariophyta [Pr–18]	U
		Labyrinthulata [Pr–19]	U
		Plasmodiophora [Pr–20]	U
		Oomycota [Pr–21]	M, M’>U
	Isokonta	Amoebomastigota [Pr–22]	U
		Myxomycota [Pr–23]	U>M”
		Pseudociliata [Pr–24]	U
		Haptomonada [Pr–25]	U
		Cryptomonada [Pr–26]	U
		Eustigmatophyta [Pr–27]	U
		Chlorophyta [Pr–28]	U=M
	Akonta	Haplospora [Pr–29]	U
		Paramyxa [Pr–30]	U
		Actinopoda [Pr–31]	U
		Gamophyta [Pr–32]	U
		Rhodophyta [Pr–33]	M>U
	Opisthokonta	Blastocladiomycota [Pr–34]	U>M
		Chytridiomycota [Pr–35]	U, M’>M
		Choanomastigota [Pr–36]	U
ANIMALIA	Placozoa	Placozoa [A–1]	U
		Myxospora [A–2]	U
	Parazoa	Porifera [A–3]	U=M’
		Coelenterata [A–4]	M>U
		Ctenophora [A–5]	U

ANIMALIA cont.	Eumetazoa	Acoelomates	
		Gnathostomulida [A–6]	U
		Platyhelminthes [A–7]	U
		Rhombozoa [A–8]	U
		Orthonectida [A–9]	U
		Nemertina [A–10]	U
		Pseudoceolomates	
		Nematoda [A–11]	U
		Nematomorpha [A–12]	U
		Acanthocephala [A–13]	U
		Potifera [A–14]	U
		Kinorhyncha [A–15]	U
		Eumetazoans, body cavity not yet characterized	
		Priapulida [A–16]	U
		Gastrotricha [A–17]	U
		Loricifera [A–18]	U
		Entoprocta [A–19]	U
		Coelomates Protostomes	
		Chelicerata [A–20]	U
		Mandibulata [A–21]	U
		Annelida [A–22]	U
		Sipuncula [A–23]	U
		Echiura [A–24]	U
		Pogonophora [A–25]	U
		Mollusca [A–26]	U
		Tardigrada [A–27]	U
		Onychophora [A–28]	U
		Lophophorales	
		Bryozoa [A–29]	M
		Brachiopoda [A–30]	U
		Phoronida [A–31]	U
		Deuterostomates	
		Chaetognatha [A–32]	U
		Hemichordata [A–33]	U
		Echinodermata [A–34]	U
		Chordates	
		Urochordata [A–35]	U=M’
		Cephalochordata [A–36]	U
		Craniata [A–37]	U
FUNGI		Microspora [F–1]	U
		Zygomycota [F–2]	M>U
		Glomeromycota [F–3]	M’, U
		Ascomycota [F–4]	M>U
		Basidiomycota [F–5]	M>U
		Lichenes [F–6]	M>U
PLANTAE	Bryata	**Bryophyta** [Pl–1]	M
		Hepatophyta [Pl–2]	M
		Anthocerophyta [Pl–3]	M’
	Tracheata	**Lycophyta** [Pl–4]	M
		Psilophyta [Pl–5]	M
		Sphenophyta [Pl–6]	M
		Filicinophyta [Pl–7]	M
		Cycadophyta [Pl–8]	M
		Ginkgophyta [Pl–9]	M
		Coniferophyta [Pl–10]	M
		Gnetophyta [Pl–11]	M
		Anthophyta [Pl–12]	M

Table 3. Taxa with features of modular organization (bold) (Belyakova et al. 2006; Maddison & Schulz 2007).

Imperia	Kingdom	Divisio (Phylum)
Eubacteria	Gracilicutes	Cyanobacteria, **Actinomycetes**
Excavates	Euglenobiontes	Acrasiomycota
Rhizaria	Cercozoa	Chlorarachniophyta
Unicontes	Mycota	Chytridiomycota, **Zygomycota**, **Ascomycota**, **Basidiomycota**
	Myxomycetae	Myxogasteromycota
	Animalia	**Coelenterata**, **Bryozoa**, **Urochordata**
Chromalveolates	Straminopilae	**Oomycota**, **Ochrophyta**
Plantae	Rhodophytes	**Rhodophyta**
	Viridiplantae	Chlorophyta, **Charophyta**
	Embryophytes	**Rhyniophyta**, **Lycopodiophyta**, **Equisetophyta**, **Polypodiophyta**, **Pinophyta**, **Magnoliophyta**

can only be seen in organisms with the two most abundant metabolism types (chemo-organo-heterotrophes and photo-litho-autotrophes).

Ecomorphological diversity

An analysis of modular organisms also shows a considerable diversity of ecomorphs. The characteristics of the abundance of the modular and unitary organization in the main groups of ecomorphs segregated by U.G. Aleev are established (Aleev 1986) (Tab. 4). This system of ecomorphs embraces all groups of living organisms and considers the most universal features. The 'autophaneron' division has been examined. It unites cell organisms which metabolic processes are carried out by means of their own fermentation and biosynthesizing systems that are in a metabolically active state (Aleev 1986). The features used to segregate phyla, classes and cohorts are shown in Table 4.

The analysis of the ecomorph spectrum shows:

• Typical unitary organisms can be found in all groups of ecomorphs. There are groups in which only unitary objects are abundant, but there are no groups in which only modular objects are present. The 'hygrobaso-ephapto-adson' cohort is close to that. Unlike its other two adjacent groups it assumes a sufficient body differentiation along with adsotrophic feeding (nutrition) and an adequate lifestyle. However, even there (for example, parasitic algae – Peridinea (*Oodinium*)), unitary organization is revealed. A modular structure is not manifested on a macromorphological level in some crustose lichens from this group.

• The modular organization is much more common in the adson phylum (Aleev 1986; Shafranova 1990). Many organisms in this group have comparably large body sizes.

• Modular organization occurs almost exclusively in attached organisms. Some species of the genera *Tillandsia*, *Salvinia* and *Riccia* represent unattached adsotrophic organisms with a passive movement style. According to some features, parasitic crustaceans from the genus *Dendrogaster* are close to modular organisms (Aleev 1986). Among organisms, which are able to move actively, only syphonophores, mobile bryozoans (*Cristatella*) and corals (*Pennatularia*) have some features of modular organization. Poorly specialized movement forms are characteristic of the latter two (Aleev 1986). Thus, modular organization is widely spread in organisms with adsotrophic feeding and an adequate lifestyle. In other systems of ecomorphs, the growth type is used for separating cohorts (Leontiev & Aculov 2004).

Table 4. Characteristics of the distribution of living objects with modular and unitary organization in various ecomorphological groups. M – modular, U – unitary organization. Ecomorphological groups taken from Aleev (1986). Types of ecomorphs segregated on the basis of nutrition: phagon – phagotrophic, adson – adsotrophic; classes segregated by the ability of the organisms to move: ephapto – attached organisms, plano – organisms that are able to move; cohorts of attached organisms segregated based on the characteristics of the relationship between the body and the substrate (baso – submerged in substrate, hygrobaso – partially submerged, hygro – located on the surface of the substrate); organisms that are able to move segregated by the type of movement (acineto – passive traveling, cineto – active traveling). Other labels are the same as in Table 1.

Division	AUTOPHANERON									
Phylum	PHAGON					ADSON				
Classis	PLANO-PHAGON		EPHAPTO-PHAGON			PLANO-ADSON		EPHAPTO-ADSON		
Cohort	cineto	acineto	baso	hygrobaso	hygro	cineto	acineto	baso	hygrobaso	hygro
Picture										
M	M’ *Siphono-phora* M” *Cristatella*	M’ *Dendro-gaster Thompsonia*	—	M” Cestoda	**M**	M” Myxo-bacteria *Oscillatoria*	**M** *Tillandsia Salvinia*	**M**–M’ *Rafflesia Sacculina* Exo-basidiales	**M** Crustose lichens	M” *Gregarina*
U	U	U	U	U	U	U	U	U	U *Oodinium fritillariae*	U
Frequency	U>>M’	U>>M’	U	U	U>M	U	U>M	M>U	M>>U	U>M”

Structural organization type

Living objects with modular organization demonstrate a huge variety of structural organization types (Tab. 5). There are unicellular and multicellular organisms, colonies of multicellular organisms and symbiotic associations (Lichenes) among them. Some features of individual objects of the population level are close to modular organisms.

Modular or close to modular forms are found among cellular organisms like mycelial fungi (Oomycetes, Zygomycetes), Actinomycetes, siphonal algae (Siphonophyceae) and colonial infusoria (Peritricha, Suctoria).

It is more difficult to find examples of plasmodia with modular organization. Apparently, this is connected with a rapid rate of formation and a short time of existance in this stage. In consequence of a modular structure, plasmodium species of the genus *Ceratomyxa* are closer to modular objects.

Ramulous aggregate colonies show some similarities to modular objects because they grow due to mucus and less commonly due to cytoplasmic chords. ‘Slimy’ colonies can be found in various groups of algae, bacteria and cyanobacteria as well as protozoa (*Spumillaria, Conochilus*) (Beklemishev 1964). The developmental program of such colonies is less self-integrated than in typical representatives of the organismic level with modular organization. However, in some cases a rather distinct algorithm of branching and a clear localization of division processes can be observed. Examples can be found in mucus (aboraceous colonies *Bacterium ramigerum* (*Bacteriaceae*)), in *Mischococcus confervicola* (Xanthophyta), in species of *Sphaerotilus*

(Chlamydobacteriaceae), *Rivularia* (Cyanobacteria), *Licmophora* (Bacillariophyta), *Hyalobryon* and *Dinobryon* (Chrysophyta). As a rule, the number of elements of the colony is fixed in cases of closer contacts within the aggregate (cytoplasmic connections) and the development of the colony is rather quick. These objects appear to be more closer to unitary forms.

Level of morphological and anatomical differentiation

Morphological and anatomical separation of modular organisms' bodies varies. The evaluation of the level of functional and structural differentiation is of special interest. It can be identified by the investigation of the structural level of the elementary module (Shafranova 1990), by investigating the presence or absence of structural and functional subsystems within the body (for example, a root system or a shoot system in higher plants), as well as by studying the possibility to separate structural units of rather high ranking in structural hierarchy on a macromorphological level (for example, the presence of partial bushes) (Gatsuk 1974, 1994, 2008a, b). The characteristics of structural differentiation in various taxa with features of modular organization are shown in Table 5. Elementary modules have different levels dependent on internal or external segregation.

The largest diversity of elementary module structure can be seen in multicellular organisms (Tab. 5). Here, the structure of modules in multicellular colonial organism (for example in ascidium) is closer to organismic structure.

Within cellular organization it is also possible to identify organisms with morphologically unsegregated elementary modules (Actinomycetes, Zygomycetes and Oomycetes) and objects with a low level of elementary module segregation (Caulerpaceae, Peritricha). The tendency for segregation in the elementary module can be found in symbyotic associations. Some lichens (*Cladonia* spp.) have complexly ramified podetia with phylloclades.

Examples of functional and structural differentiation of the body into two sub-systems can be noticed in different types of structural organization and in different versions of the structure of the elementary module. The extent of such differentiation varies.

• Cellular organization level: systems of rhizoidal elements and the system of vertical thallus axes in Caulerpaceae; the system of elements of substrate mycelium and arial mycelium in Actinomycetes; the 'stem' part and the 'crown' in *Zoothamnion* (Peritricha).

• Multicellular organisms: protonema and the system of gametophores in bryophytes, the root and shoot system in higher plants and the system of stolons and shoots in colonial animals.

• Symbiotic associations of lichens: primary thallus and podetia.

Analogues of partial bushes in a cellular organization type can be found in *Mucor stolonifer*, *Rhizopus nigricans* (Cherepanova 1981) and in some lichens from the subgenus *Cladinia* (Oksner 1974; Ahti 2000).

Level of integrity of living systems

Living organisms with modular organization demonstrate a wide variety of objects with various levels of integrity. This makes the problem of searching individuals with modular organization virtually unsolvable (Beklemishev 1964; Marfenin 1993a). Level of wholeness is an integral characteristic that is defined by various groups of criteria. In general, two main levels can be separated – organismic and over-organismic (Aleev 1986).

Table 5. Characteristics of structural differentiation in taxa with signs of modular organization. Other labels the same as in Table 1.

Structural level of the elementary module	Cell part	Cell	Multicellular module: Morphologically not separated, separated into tissues	Multicellular module: Separated into organs	Multicellular module: Separated into organ systems	Metabionting organism	Monobionting organism	Part of metabionting organism and monobiont
TAXA: PROCARYOTA	**ACTINOMYCETES**	CYANOBACTERIA Stygonematales				CYANO-BACTERIA *Rivularia* M”	Chlamydobacteriaceae M” Bacteriaceae M”	Streptomyces+ *Chlorella xanthella* M”
TAXA: FUNGI	M Y C O T A Chytridiomycetes M’ Oomycetes **Zygomycetes** Trichomycetes M’ MYXOMYCOTA M”	**A s c o m y c e t e s** **B a s i d i o m y c e t e s**						L I C H E N E S **Cladoniaceae** **Stereocaulaceae**
TAXA: PLANTAE	C H L O R O P H Y T A Siphonophyceae	**CHAROPHYTA** **P H A E O P H Y T A**	**B R Y O P H Y T A**				Chrysomonodaceae M” Volvocaceae M”	
	X A N T H O P H Y T A Xanthosiphonophyceae M’	Xanthotricho-phyceae **R H O D O P H Y T A**	Rafflesiaceae Podostemaceae	**M A G N O L I O - P H Y T A**			XANTHOPHYTA Licmophora M” (Bacillariophyta)	
TAXA: ANIMALIA	CILIOPHORA Succtoria Peritricha		PORIFERA M’ **COELENTERATA**	TENTACULATA Kamptozoa Pyrosoma M’ H E M I C H O R D A T A CHORDATA: **Ascidiae**		Conochilus, *Rotatoria* M”	Spumillaria Radiolaria M”	
Type of structural organization	Unicellular organism, plasmodium	Multicellular organism	Multicellular organism-colony			Aggregate colonies		Symbiotic association
Level of structural integration	Mono-biont / Metabiont	Metabiont	Coenometabiont			Coenometabiont		Coenosis

Within each type of structural organization, there is also a wide variety of objects of different integrity. Thus, on a cellular organization level, for example in colonial peritrichous infusoria, there are temporary colonies quickly falling apart into traveling and more stable colonies. Among the latter ones, individual zooids (*Epistylis, Operculata*) or the entire colonies (*Carchesium, Zoothamnion)* are able to respond to stimulation. The variety of forms with various levels of integrity is even bigger in multicellular modular organisms. Very low levels of integrity are seen in sponges, which, due to their weak differentiation of morphogenetic cycles and modules, aren't always accepted as modular organized. A significantly larger integrity can be found in Tunicata colonies, as well as in young and woody flowering plants.

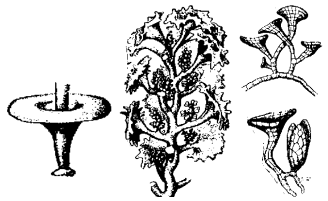
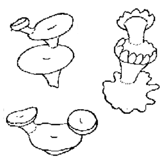
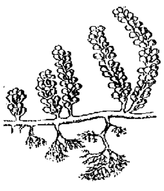
In symbiotic lichen associations all the transitions from temporary facultative lichens and 'semi-lichens' to forms in which the morphogenetic role of the phycobiont is expressed like that of mycobionts (for example, some mucous lichens) can be observed (Oksner 1974). Many lichens get closer to an organismic level of integrity due to some features (Oksner 1974; Aleev 1986). This assumption is supported by the rather complex regulation systems of physiological interactions between the components of the lichen. Some aggregate colonies have an intermediate position between organismic and over-organismic levels.

Thus, living organisms with modular organization are characterized by various types of metabolism, considerable taxonomical, ecomorphological and structural diversity. They represent forms with different types of structural organization and various degrees of complexity and integrity. The available material gives a unique basis for large-scale structural, functional, morphogenetical and ontogenetical studies. The diversity of structures being similar in construction and function and originating from different basic constructs allows to derive common patterns of morphogenesis and semophylesis of similar structural elements and their systems, as well as to clarify the main modus of structural evolution.

Modular organization as an object of structural, morphogenetical and ontogenetical research

Modular organisms have a wide spectrum of shoot-like structures (Tab. 6). The differentiation into axial and appendicial elements in adsotrophic and phagotrophic organisms, in autotrophes and heterotrophes and representatives of different kingdoms of the organic world can be observed (Tabs 1–3). Shoot-like systems are very common in photosynthesizing plants. Sometimes, more complex systems with an outer appearance similar to a shoot with leaves are formed (for example, the phylloclade in *Ruscus* and *Asparagus*). To some extent, branches of colonial hydroids and bryozoans look like shoots. An even bigger similarity to shoots can be found in patulous pinnate colonies with flattened side branches that look like plant leaves. It is not a coincidence that terms like shoots, stolons, branches, etc. are common in the descriptive morphology of these objects (Marfenin 1993a, b). In this case a more complex system of zooids looks like a leaf-like structure. It is more difficult to find examples of shoot-like structures in mushrooms (Serebryakov 1952). To some extent, elements of the fruit body of *Hericium* (Tab. 6) and individual species of Clavariaceae are similar to shoots. A much bigger similarity to shoots can be found in the podetium of *Cladonia* species (Tab. 6). Lateral lamellar structures – phylloclades – can be formed on the cylindrical and scypha-like axes of the podetium (Oksner 1974; Ahti 2000). They are very characteristic of species with larger podetia. They considerably enlarge the assimilating surface. *Stereocaulon*

Table 6. Scypha-like and shoot-like structures at different levels of structural organization.

	ANIMALIA	PLANTAE	FUNGI	ANIMALIA	LICHENES
Scypha-like structures					
Shoot-like structures					
Levels of structural organization	Unicellular organism	Multicellular organism		Multicellular colonial organism	Symbiotic association

species form flattened axis-branches that are also commonly called phylloclades (Dombrovskaya 1996). Felt structures are formed on the surfaces of pseudpodetia of the representatives of the genus *Stereocaulon*. These structures are typical of open environments. They are like an analogue of indumenta in plants (Dombrovskaya 1996; Plusnin 2004). Thus, in addition to the exterior resemblance, there are also common functional, morphogenetical and ecomorphological traits. It is also interesting to note that the shoot-like structures presented in Table 6 are formed on different levels of structural organization. The most original shoot-like structures are seen in Siphonales algae, which have no cellular structure.

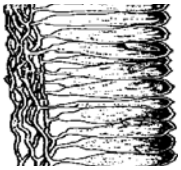
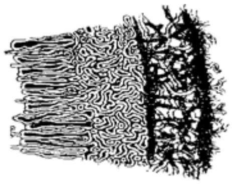
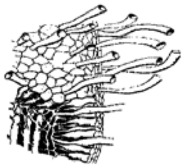
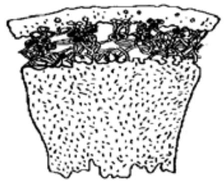
Red and brown algae's similarity to leaves increases due to structures that look similar to veins (Serebryakov 1952; Fedorov & Takhtajan 1974–1982). Brown algae have specialized sieve tubular scypha.

Funnel-shaped structures are also found in different taxa and at different structural organizational levels. Table 6 shows examples from protozoans (except infusorium), algae, higher plants (protonema of the *Diphyscium* moss), fungi and colonial bryozoans. This structural element is very common in lichens of the genus *Cladonia* (Oksner 1974; Ahti 2000).

A wide spectrum of tissue-like formations can be observed (Tab. 7). In many cases, the axial structure could be divided into the core and the pith. Moreover, elements of these topographical zones may be cell parts (in Siphonales), multicellular micellar chords (in higher fungi), zooids and other colonial elements (in hydroid polypus), multicellular micellar chords and an algal zone (in lichens).

Wide spectra of similar macromorphological and anatomical structures that are observed in different groups of living organisms may become a good basis for complex studies on morphogenesis, growth processes and ontogenetic programs. Such research will substantially widen our perceptions of the main mechanisms of morphogenesis and schemes of ontogenesis, as well as types of ontogenetical programs. Currently, the research of analogues in the structural

Table 7. Tissue-like formations at different levels of structural organization.

	PLANTAE	FUNGI	ANIMALIA	LICHENES
Structural unit	Cell part	Multicellular micellar chord	Zooids and other colonial elements	Multicellular micellar chords and algal zone
Tissue-like formations				
Levels of structural organization	Unicellular organism	Multicellular organism	Multicellular colonial organism	Symbiotic associaion

and functional organization of the growth systems of objects at different levels of structural organization in different kingdoms of living organisms is of special interest. One of the most interesting objects are symbiotic lichen associations, which are close to the organismic level in their level of integrity. The analysis of morphogenesis of *Cladonia* shows that some species have rather complex systems of meristematically active tendencies. They are formed as a result of the differentiation of the initial circle-like or dome-like primordium (Hammer 1996, 1997, 1998, 2000, 2001). The morphogenetic system of lichens assumes a consistent apical growth of hypha chords with the subsequent reproduction and differentiation of the elements of the algal zone. The fact that some bush-like lichens have complex systems of structural units makes them a convenient model object in studies on the specifics of complicated hierarchical morphogenetic development programs in symbiotic associations that are analogous in their differentiation level to some vascular plants with intricately segregated bodies.

It is impossible to find objects within an unitary organization having the same plasticity of ontogenesis and instability of structure like modular objects. In this sense, lichens and bryophytes are most interesting. Among them there are representatives with a considerable body differentiation on the macromorphological level and a complex system of structural units (for example, lichens from the subgenus *Cladinia, Climacium dendroides*) (Notov 2004b, c; Ivanova & Notov 2005). In this case, however, the structural and functional differentiation is much less determined than in vascular plants with a system that is comparatively high in complexity and architectural model. For example, all types of characteristic structural units of *Climacium dendroides*, which has a more strictly defined architectural model than other bryophytes, can be seen under various conditions and with different frequency within its 'head' (Notov 2004b). The presence of similar architectural models in modular objects of different organizational level opens wide opportunities for researching the dependence of the ratio of structural and functional plasticity to the organizational level. Such studies need further development in the previously presented methods of functional and dynamic macrostructure analysis of modular objects (Marfenin 1993a, b).

Modular organization is a convenient model object in studies connected with various aspects of reproductive biology (Notov 2010). Open growth of modular living beings defines the unity of morphogenesis and processes of reproduction. Repeatedly recurring reserves of stem cells and high levels of toti-pluripotency in multicellular modular organisms make a wide dissemination of vegetative and asexual reproduction possible (Batygina 2010; Isaeva 2010; Isaeva & Batygina 2010). The multiplicity of development is manifested at different levels of structural hierarchy. In contrast to unitary organisms, modular organisms are characterized by a variety of methods and types of reproduction and breeding, a variety of life cycles, a significant frequency of occurrence of complex life cycles with an alternation of generations (forms of development) (Tab. 8) (Zhukova 1983; Notov 2010). These features are a result of the close interrelationship between embryogenesis and morphogenesis, growth processes, reproduction and regeneration, that occur on the basis of continuously operating meristems. The wide range of different methods and types of breeding and reproduction defines the system of backup ways that ensure the reliability of reproduction and diversity of additional redundant structures and processes (Batygina 1994; Batygina & Vasilyeva 2002). Currently, further cross-spectrum analysis is central for reproductive systems and processes in different groups of modular organisms.

Modular organization as an object of general biological research

A comparison of modular and unitary objects allows to recognize not only the specific features of living organisms with different organization types, but also to discover numerous analogues indicating common principles of organization in different living systems. The following analogues in organization, functioning and individual development of modular and unitary objects are:

• The growth algorithm of modular organisms may be matched with the construction plan of unitary organisms.

• The form-building sub-system of modular organisms is an analogue of the controlling sub-system of unitary organisms.

• The phytocoenotype of modular organisms is somewhat similar to the temperament type of unitary organisms (see: Yurtsev 1986).

• Plastic ontogenesis of modular organisms 'imitates' the behavior of unitary organisms.

• The shifting of centers with maximum physiological activity like the growth of modular objects is an active movement of unitary organisms.

• An organism of modules is to some extent similar to a population of unitary organisms.

Such analogues demonstrate the general principles and tendencies of the transformation of living systems. Depending on the organization type these principles and tendencies are realized differently.

The analysis of unitary and modular objects also allows to uncover some general tendencies of evolutionary transformation. The increase in the level of integrity of morphogenesis and ontogenesis is one of the general directions of the evolution of living organisms. In the process of its realization in modular objects it is possible that some features similar to the unitary organization will be formed. This could be, for example, the possibility to isolate the steps of the creation and functioning of the system, as well as a higher integrity of the terminal process. Among modular objects, this tendency is almost completely realized in some monocarpic plants. Within modular organization it is possible to reach a high integrity of morphogenetic processes at the level of individual structures. In plants, these structures can be buds (especially preformed ones), leaves, flowers, specialized peduncles, and in animals zooids. Besides, the similarity to features of unitary objects increases due to the stabilization of the number of elements (e.g., flowers).

Similarity to unitary objects may be formal in some features. For example, the stability of the number of structural units and the relative stability of the system limits are possible on the basis of modular organization if there is a high equilibrium of formation and dying processes (in some corm plants and vegetatively mobile annuals). A functional analysis of such objects and typical unitary organisms allows to establish a different organizational basis for the noted similarities.

Deep transformations of modular organization that increase the similarity to unitary objects are possible (Notov 2009). For example, the increase in the intensity of asexual reproduction combined with advanced reductionalistic processes may lead to the loss of the typical modular construction (representatives of Lemnaceae). In this case, the physical connection between modules is so brief and the shoot structure, which is typical of flowering plants, is lost to such an extent that it may be concluded that 'secondarily unitary' objects are formed. These objects are very similar to the unitary population.

Thus, central problems of contemporary theoretical biology are to clarify the specific ways of solving functional tasks, ways of realizing general tendencies, and the degree of dependence of the specific characteristics on a definite organization type. The analysis of this problem will bring us closer to an understanding of the the essence of the common organization principles and the evolution of living organisms.

Modular organization as an object of systems research

Recently there has been a return of interest in systems studies (Takhtajan 2001; Urmantsev 2008). Integrative processes that facilitate the integrity of biological systems are still studied insufficiently. Non-centralized self-regulation of a colonial organism of a hydroid is an interesting model object for cybernetics and the neuron network theory. It adds considerably to the perceptions of the principles of self-organization of living organisms (Marfenin 2002). The formulated principles of obtaining organismic integrity in hydroid polyps unveil the essence of one of the cybernetic strategies of living systems (Marfenin 2002). Multiple structural duplication characteristic of living beings at all organizational levels (molecular, cellular, multicellular, populational, ecosystematical and biosphere) is realized at the level of a modular organism. It facilitates another regulating scheme, if it is compared to unitary objects (Marfenin 2002).

The analysis of individual development, the system of reproduction and breeding of modular organisms is interesting from the synergetic the point of view (Notov 2005a, b, 2006). Open growth and block ontogenesis allow to consider embryogenesis of modular organisms as one of the elements of the morphogenetic system, which is implemented during individual development. The synergetic character of reproduction and breeding is clearly seen in taxa with a higher level of organization. By this reason, the comparison of reproductive systems of seed plants and tunicates, especially ascidium has to be drawn (see Notov 2006, 2010).

Currently, the analysis of the organization of living organisms based on the idea of fractals (Tchaikovsky 2006; Isaeva et al. 2007) plays a central role. In connection with the modular organization type this approach is especially effective in analyzing modular objects with a complex hierarchical system of structural units (Gatsuk 1994, 2008a; Shafranova & Gatsuk 1994; Notov 2001, 2004a). Units of different ranks of structural organization are self-similar from the point of view of general structure and function traits, but they are different in the extent of the definiteness of their composition and level of autonomy. Self-similarity of macromorphological

Table 8. Main versions of life cycles in different taxa of modular organisms. H – haplobiont, D – diplobiont, DC – dicaryobiont, > – form is dominant, ( ) – bionts are connected, [ ] – with vastly changed organization or secondary unitary organisms. Names of genera and larger taxonomical units are given in small letters, their ending are taken off (-phyta – in algae and higher plants, -mycota – in fungi and fungi-like organisms). Names of groups that belong to higher fungi and plants are underlined. Triangles signify versions of life cycles of representatives with unitary organization. The size of this symbol reflects the frequency of occurrence. Other labels are in the text.

CHARACTERISTICS	TWO NUCLEAR PHASES											THREE NUCLEAR PHASES		
	Without change in development form		With change of the development form (generations)									Without change	With change	
			With unstable change	With stable change									With stable change	
				Two diplobionts	Two different forms of development (generations)					Three or more forms			2 forms	3 or more
					Independent bionts			Connected bionts		Different autonomy level			Different autonomy	
FORMULA	D D2*	H	D, D, H	$D_1 > D_2$ $(D_2 > D_1)^*$ $(D_1 > D_2)^{**}$	D, H	D>H	H>D	(D>H)	(H>D) $(H>D_1)^*$	$(H>D_1), D_2$; $(H>D_1, D_2), D_2$	$(H>D_1), D_2$ $(H>D_1)> D_2^*$ $D_2, H_♂ >$ $H_♀^{**}$	DC	(H>DC)* (H<DC)	$(H<DC_1)$, DC_2, DC_3
PLANTAE	CHLORO PHAEO *Fucus* ▲	CHLORO *Ulothrix* CHARO ▲	PHAEO *Ectocarpus* CHLORO *Ulva*		CHLORO *Ulva* PHAEO *Dictyota*	CHLORO *Derbesia* PHAEO *Laminaria* TRACHEO	CHLORO *Monostroma* PHAEO *Cutleria*	TRACHEO	BRYO RHODO *Liagora**	RHODO *Audouinella gynandra*	RHODO *Polysiphonia* *Lemanea* *Nemalion** *Palmaria***			
FUNGI	OO *Saprolegnia* ASCO [*Saccharomyces*]	ZYGO *Mucor* ▲	CHYTRIDIO* Blastocladiales		CHYTRIDIO *Allomyces*				ZYGO *Rhizopus*			BASIDIO *Ustilago*	ASCO* BASIDIO	BASIDIO *Puccinia*
ANIMALIA	CNIDARIA [*Pelagia*]* BRYOZOA CHORDATA Ascidiaea ▲	▲		CNIDARIA *Obelia* *Bougainvillea** Coronata** CHORDATA Salpae	▲									

structural units of any level is manifested in the presence of a form-building subsystem. Self-organization of units, which have a higher rank than an elementary metamere, influences structural (plurality, equivalence, multifunctionality of uniform units) and functional (ensuring reliability by cold reserving, regulation role of the form-building subsystem) aspects of organization as well as developmental features (low degree determinacy of small cycles and multivariant development). The question of organizational similarity of structures with modular construction and open growth at dependent levels of structural hierarchy needs separate analyses (Notov 2001).

Interesting results can be obtained from a special analysis of the proposed epistemological concepts and approaches that strive to reflect the ontological essence of objects with modular organization correctly. Such research in systematics and morphology are gaining in special importance (Notov 2007).

Thus, the concept of modular organization may be seen as a mean of developing the theoretical apparatus of biology and as an instrument for detailed organizational analysis of living beings. Uncovering common patterns (that are a result of systematic similarity in particular representatives of different taxa with modular organization types) is very important for the development of various areas of theoretical biology and systems analysis.

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References

Ahti T. (2000): *Cladoniaceae*. – Flora Neotropica, Monograph 78. – New York: New York Botanical Garden.

Aleev Y. G. (1986): Ecomorphology. – Kiev: Naukova Dumka. [In Russian]

Alimov A. F. [ed.] **(2000):** Protista: Handbook on Zoology. – St. Petersburg: Nauka. [In Russian]

Batygina T. B. (1994): Ovule and seed from the angle of reliability of biological systems. – In: Batygina T. B. [ed.]: Embryology of flowering plants: Terminology and concepts. Vol. 1. Generative organs of flowers: 263–266. – St. Petersburg: Mir i Sem'ya. [In Russian]

Batygina T. B. (2010): Stem cells and morphogenetic developmental programs in plants. – In: Hitomi A. & Katoaka M. [eds.]: Daughter cells: properties characteristics and stem cells: 51–128. – New York: Nova Science Publishers.

Batygina T. B. & Vasilyeva V. E. (2002): Plant propagation: Textbook. – St. Petersburg: University Press. [In Russian]

Beklemishev V. N. (1964): Comparative anatomy of invertebrates. – Moscow: Nauka. [In Russian]

Belyakova G. A., Diyakov Y. T. & Tarasov K. L. (2006): Algae and Fungi. – Moscow: Izdat. Tsentr. Akademiya. [In Russian]

Cavalier-Smith T. (2002): The phagotrophic origin of eukaryotes and phylogenetic classification of Protozoa. – Int. J. Syst. Evol. Microbiol. **52**(2): 297–354.

Cavalier-Smith T. (2003): Protist phylogeny and the high-level classification of Protozoa. – European Journal of Protistology **39**(4): 338–348.

Cherepanova N. P. (1981): Morphology and reproduction of fungi. – Leningrad: University Press. [In Russian]

Dombrovskaya A.V. (1996): Genus *Stereocaulon* in the former USSR. – St. Petersburg: Mir i Sem'ya. [In Russian]

Fedorov A.A. & Takhtajan A.L. [eds.] **(1974–1982):** Plant life [Vol. 1–6]. – Leningrad: Nauka. [In Russian]

Gatsuk L.E. (1974): Gemmaxylare plants and the hierarchical system of units of their shoots. – Bjull. Mosk. Obsh. Ispyt. Prir., otd. biol. **79**(1): 100–113. [In Russian]

Gatsuk L.E. (1994): The hierarchical system of structural and biological units of a plant organism defined macromorphologically. – In: Elenevsky A.G. [ed.]: Progress in ecomorphology and its influence on related sciences: 18–19. – Moscow: Prosveshenie. [In Russian]

Gatsuk L.E. (2008a): The plant organism: an experience of constructing a hierarchical system of its structural and biological units. – In: Contemporary approaches to describe plant structure: 26–47. – Kirov: Loban'. [In Russian]

Gatsuk L.E. (2008b): Unitary and modular live beings: about the history of conception. – Vestnik TGU. Ser. Biology and Ecology **9**(25/85): 29–41. [In Russian]

Hammer S. (1996): Modular growth in verticillate podetia of *Cladonia*. – Mycologia **88**: 533–538.

Hammer S. (1997): Branching dynamics in *Cladina subtenuis*. – Mycologia **89:** 461–467.

Hammer S. (1998): Form, convention, and evolution in *Cladonia*: The challenge of lichen developmental morphology. – In: Glenn M.G., Harris R., Dirig R.C. & Cole M.S. [eds.]: Lichenographia thomsoniana: North American lichenology in honor of John W. Thomson: 5–19. – New York: Mycotaxon Ltd.

Hammer S. (2000): Meristem growth dynamics and branching patterns in the *Cladoniaceae*. – Amer. J. Bot. **87**(1): 33–47.

Hammer S. (2001): Lateral growth patterns in the *Cladoniaceae*. – Amer. J. Bot. **88**(5): 788–796.

Isaeva V.V. (2010): The diversity of ontogeny in animals with asexual reproduction and plasticity of early development. – Ontogenez **41**(5): 340–352. [In Russian]

Isaeva V.V. & Batygina T.B. (2010): Similarities and differences of plant and animal stem cells. – In: Biology of development: morphogenesis of reproductive systems and role of somatic, stem cells in ontogenesis and evolution: Materials of the International Conference dedicated to the 50th anniversary of the embryology and reproductive biology laboratory of BIN RAN (December 13–16, 2010): 64–66. – St. Petersburg: KMK. [In Russian]

Isaeva V.V., Karetin Y.A., Pushena E.V., Chernyshov A.V. & Presnov E.B. (2007): Fractals and chaos in biological morphogenesis. – In: Cellular, molecular and evolutionary aspects of morphogenesis: symposium with international participation (Moscow, October 9–11, 2007): 68–70. – Moscow: KMK. [In Russian]

Ivanova O.V. & Notov A.A. (2005): Variability of the structure of *Cladonia gracilis* (L.) Willd. in different habitats. – In: Dementieva S.M. [ed.]: Biology Department: Proceedings of the conference of graduate and post-graduate students, 28th April, 2005: 15–21. – Tver: Tver State University. [In Russian]

Khokhryakov A.P. (1997): Plants as modular organisms. – In: Proceedings of the 3rd international conference on plant anatomy and morphology: 371–372. – St. Petersburg: Diada. [In Russian]

Kuznetzova T.V. (1992): On the complementary approach to morphology of inflorescences. – Bot. Zhurn. **77**(12): 7–24. [In Russian]

Kuznetzova T.V. (1995): On the history of studies of the shoot structure of vascular plants. – Bot. Zhurn. **80**(7): 1–11. [In Russian]

Leontiev D.V. & Akulov A.Y. (2004): Ecomorpheme of the organic world: experience of construction **–** Zhurn. Obshchei Biol. **65**(6): 500–526. [In Russian]

Lodkina M.M. (1983): Features of morphological evolution conditioned by the specific ontogenesis of plants. – Zhurn. Obshchei Biol. **44**(2): 239–253. [In Russian]

Maddison D. R. & Schulz K.-S. (2007): The Tree of Life Web Project. – http://tolweb.org [20.03.2011].

Marfenin N. N. (1993a): The phenomena of colonial organization. – Moscow: Moscow State University. [In Russian]

Marfenin N. N. (1993b): Functional morphology of colonial hydroids. – St. Petersburg: ZIN RAN. [In Russian]

Marfenin N. N. (1999): The development of modular organization conception. **–** Zhurn. Obshchei Biol. **60**(1): 6–17. [In Russian]

Marfenin N. N. (2002): Decentralized self-regulation of the integrity of colonial organisms. **–** Zhurn. Obshchei Biol. **63**(1): 26–39. [In Russian]

Margulis L. & Chapman M. J. (2009): Kingdoms & Domains: An illustrated guide to the phyla of life on earth [4th ed.]. – Amsterdam: Academic Press, Elsevier.

Notov A. A. (1997): On the development of the system of structural units in different groups of modular objects. – In: Proceedings of the 3rd international conference on plant anatomy and morphology: 362–363. – St. Petersburg: Diada. [In Russian]

Notov A. A. (1999): On the specificity of functional organization and individual development of modular objects. – Zhurn. Obshchei Biol. **60**(1): 60–75. [In Russian]

Notov A. A. (2001): The concept of modular organization and the problem of organizational polymorphism at different levels of the structural hierarchy of living organisms. – In: Oskolski, A. A., Sokolov D. D. & Timonin A. K. [eds.]: Homologies in botany: Experience and reflections: Proceedings of the IXth workshop on theoretical plant morphology 'Types of similarities and principles of the homologies revealed in plant morphology': 119–128. – St. Petersburg: St. Petersburg Association of Scientists and Scholars. [In Russian]

Notov A. A. (2004a): The concept of fractals as a way to reveal specific character of organization of higher plants. – In: Botany and botanical education: tradition and perspective. Proceedings of a research conference dedicated to the 200-year anniversary of the higher plants department of MSU (Moscow, January 26–30, 2004): 36–38. – Moscow: KMK. [In Russian]

Notov A. A. (2004b): About polyvariant morphogenesis of shoot system *Climacium dendroides*. – In: Materials of the VIIth international plant morphology conference dedicated to the memory of I. G. & T. I. Serebryakovi: 186–187. – Moscow: University Press. [In Russian]

Notov A. A. (2004c): Polyvariant morphogenesis of shoot system *Climacium dendroides* (Musci). – Growth and development of plants: Theoretical and practical problems: Abstract international scientific conference, Babtai, 7–9 June 2004: 63. – Babtai: Lithuanian Institute of Horticulture.

Notov A. A. (2005a): On functional organization and individual development of modular objects. – Wulfenia **12**: 65–85.

Notov A. A. (2005b): The synergetic aspect of individual organism development. – In: Materials of the Ist international interdisciplinary seminar in memory of corresponding member RAS S. P. Kurdumov 'Ideas of synergetics in natural sciences', April 15–17, 2005, Tver: 82–83. – Tver: University Press. [In Russian]

Notov A. A. (2006): Reproduction and replication in modular organisms from the synergetic point of view. – In: Materials of the international interdisciplinary research conference 'Ideas of synergetics in natural sciences'. April 20–23, 2006, Tver: 196–198. – Tver: University Press. [In Russian]

Notov A. A. (2007): Modular organisms as objects of systematics and morphology. – In: Artemyeva T. V. & Mikeshin M. I. [eds.]: Carolus Linnaeus in Russia: 187–189. – St. Petersburg: St. Petersburg Center for History of Ideas. (The philosophical age: Almanac 33). [In Russian]

Notov A. A. (2009): On the ways of a modular organization. – In: Tkachenko V. G. [ed.]: The collection of scientific works of Lugansk NAU: Biological sciences: 87–99. – Lugansk: Elton-2. [In Russian]

Notov A. A. (2010): Reproductive systems of modular organisms: modus and ways of rise of reliability. – Vestnik TGU. Ser. Biology and Ecology **19**(27): 29–41. [In Russian]

Oksner A. N. (1974): Morphology, systematic and geographical distribution. – In: Lichen key of the USSR. 2: 1–284. – Leningrad: Nauka. [In Russian]

Plusnin S. N. (2004): Mechanisms of supporting polymorphism in populations of the *Stereocaulon alpinum*. – Syktyvkar. (Research report Komi RC UrO RAS 446). [In Russian]

Schmalhausen I. I. (1968): Cybernetic problems in biology. – Novosibirsk: Nauka. [In Russian]

Serebryakov I. G. (1952): Vegetative organs morphology of higher plants. – Moscow: Sovetskaya nauka. [In Russian]

Shafranova L. M. (1990): The plant as a life form (On the question of the content of the concept 'plant'). – Zhurn. Obshchei Biol. **51**(1): 72–89. [In Russian]

Shafranova L. M. & Gatsuk L. E. (1994): The plant as a spatial and time metameric (modular) system. – In: Elenevskiy A. G. [ed.]: Progress in ecomorphology and its influence on related sciences: 6–7. – Moscow: Prometey. [In Russian]

Sidorova I. I. (2003): Mushroom macrosystems: methodology and changes of the last decade. – In: New in systematic and nomenclature of mushrooms: 7–70. – Moscow. [In Russian]

Sokolov V. E. [ed.] **(1987–1989):** Animal life [Vol. 1–7]. – Leningrad: Nauka. [In Russian]

Takhtajan A. L. (2001): Principia tectologica: Principles of organization of complex systems: An evolutionary approach [2nd ed.]. – St. Petersburg: SPCPA Press. [In Russian]

Tchaikovsky Y. V. (1990): Elements of the evolutionary diatropics. – Moscow: Nauka. [In Russian]

Tchaikovsky Y. V. (2006): Life development science: theory of evolution experience. – Moscow: KMK. [In Russian]

Urmantsev Y. A. (2008): General systems theory: condition, appendixes and development perspectives. – In: Practical Science. – http//www.sci.aha.ru [20.03.2011]. [In Russian]

Vorobyeva E. I. (2006): Problem of organism integrity and its perspectives. – Izvestiya RAS. Ser. Biol. **5**: 530–540. [In Russian]

Yurtsev B. A. (1986): Production strategies and life forms of plants. – In: Serebryakova T. I. & Sokolova T. G. [eds.]: Life forms in plant ecology and taxonomy: 9–23. – Moscow: Nauka. [In Russian]

Zhukova L. A. (1983): Ontogenesis and cycles of reproduction in plants. – Zhurn. Obshchei Biol. **44**(3): 361–374. [In Russian]

Address of the author:

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