Wulfenia **12** (2005): 65–85

Wulfenia

Mitteilungen des
Kärntner Botanikzentrums
Klagenfurt

Functional organization and individual development of modular objects

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Summary: The principal feature of the modular organization is the correlation between its development, functioning and regulation, and changes in the object macrostructure. Dynamic macrostructure accounts for low integrity of the system and instability of its borders. Functioning and development of modular objects are similar to those in population systems. The article presents an attempt of a functional interpretation of modular objects.

Keywords: modular organization, unitary organization, individual development of modular objects, functional organization of modular objects, organization principles, theoretical morphology

The growing interest towards modular objects (JACKSON & COATES 1986; ELLISON & HARVELL 1989; MARFENIN 1993a; SHAFRANOVA & GATSUK 1994) can be explained by the intuitive perception that the structure, functioning, evolution and ecology of the open growth organisms have much in common, although they might belong to different kingdoms of life. At the same time, according to most Russian researchers (YURTSEV 1976; LODKINA 1983; SEREBRYAKOVA 1983; SHAFRANOVA 1990; KUSNETZOVA 1992; MARFENIN 1993a; NUKHIMOVSKY 1997, 2002), the specific features of modular objects have not attracted adequate attention in theoretical biology.

Numerous attempts to reveal the general characteristics of modular organisms (BEKLEMISHEV 1950; STAROSTIN 1966, 1967; GRODZINSKIY 1974, 1983; YUSUFOV 1976; SHAFRANOVA 1990; MARFENIN 1993a,b) have proved the complexity of the task. Its solution implies structural and functional research, studies on ontogenesis, evolution and ecology of modular objects, and their analysis as cybernetic systems. By now the structural aspect of plant organisms has been studied in detail (SHAFRANOVA 1980, 1981, 1990, 1993; GATSUK 1974, 1985, 1994; SEREBRYAKOVA 1977; KUSNETZOVA 1985, 1986, 1995, 1998; SHAFRANOVA & GATSUK 1994); valid generalizations have been made about plant ontogenesis and morphogenesis (KHOKHRYAKOV 1973, 1975; YUSUFOV 1976, 1982, 1988, 1996; MAZURENKO & KHOKHRYAKOV 1977; DEMKIV 1981; DEMKIV & SYTNIK 1985; LODKINA 1983; SEREBRYAKOVA 1983); peculiarities of evolutionary changes influenced by certain ontogeneses and morphogeneses have been described (LODKINA 1983; SEREBRYAKOVA 1983). Rich data have been accumulated on the functional organization of colonial animals (MARFENIN 1993a,b). However, the data is summarized only on individual taxa of modular objects, while general peculiarities of their functional organization have been studied insufficiently. There is an urgent need to think about modular organization philosophically and to find an approach combining different researches.

We have tried to employ the dialectical method and functional approach developed by M. I. SETROV (1969, 1971a,b, 1972, 1975) in order to represent modular objects as functioning and developing living systems and to reveal their peculiarities (NOTOV 1999).

As a rule, modular organization is first of all, defined through its ability to *open growth* or *cyclic morphogenesis* and *modular structure* (TOMLINSON 1984; BIGON et al. 1989; KUSNETZOVA 1992, 1995; MARFENIN 1993a). At the same time, growth is traditionally correlated with formation (LODKINA 1983; SHAFRANOVA 1990), so both terms "open growth" and "cyclic morphogenesis", reflect the essential feature of modular organization – repeated formation of the *similar* structural blocks (modules) throughout the life of the object. The result of this type of growth (cyclic morphogenesis) is modular structure. In the case of modular organization both features (open growth and modular structure) are present on the level of a whole living object.

The two features mentioned above can manifest themselves on the level of separate structures or at a certain period of development (SHAFRANOVA 1981, 1990; NOTOV 1997, 1999, 2001; KHOKHRYAKOV 1997); besides they can be more or less pronounced, for example: open growth of nails and hair of vertebrates, mycelium forms of some fungi capable of developing yeast-like forms. There are objects with only one feature manifested on the level of an organism, for example, open growth of some lamellar algae and crustose lichens or modular structure of a starfish. In our opinion, we can speak about modular organization only if the two main features (open growth and modular structure) are distinctly pronounced on the level of an organism as a whole. In this article we are going to deal only with such objects. There are of course various intermediate cases, but they are not the subject of our study.

Usually modular and unitary organizations are illustrated by the examples of higher plants and vertebrates. We tried to point out the properties common for representatives of different kingdoms of living organisms of modular or unitary organization (Tables 1 & 2). Special attention was paid to multicellular animals and plants with definite features of modular organization and distinct patterns of their development. Fungi and different unicellular modular organisms were studied to a less extent.

In a complex reproduction cycle every stage or generation has a certain type of organization – modular or unitary. As a rule, modular organization is fully manifested only in one generation dominating the reproduction cycle (gametophyte of moss-like species, sporophyte of vascular species, polyploid stage of colonial Coelenterata). Modular organization is less common for several generations in the reproduction cycle (some algae, fungi). To reveal the peculiarities of individual development we have analyzed the generations and stages with distinct features of modular or unitary organization.

The analyzed modular and unitary objects are regarded as integral systems. In this connection their morphofunctional systems are referred to as subsystems.

Functional organization of a definitive modular object

Main aspects of organization

Structural aspect

Cyclic morphogenesis implies the differentiation of a special *form-building subsystem* that functions alongside with other subsystems of an organism (Table 1). The differentiation of such a subsystem is one of the prerequisites for modular organization. The presence of the form-building subsystem determines modular organization of an object, plurality and repetition of similar modules. The form-building subsystem is never centralized, so the processes of forming modular objects are of local character.

Table 1: Functional organization of definitive modular and unitary living systems; specific features.

Features	Modular organization	Unitary organization
Specific manifestations of the general organization principles		
Compatibility principle	In the definitive structure of an organism there is a form-building subsystem which functions alongside with other functional subsystems	In the definitive structure of an organism there is a centralized controlling subsystem
Actualization principle	Form-building processes have a pronounced functional character and are aimed not only at the conservation of a system but also at its development	Controlling processes have a pronounced functional character. The conservation and development of a system are ensured by the controlling subsystem
Concentration principle	The form-building subsystem combines all the functional subsystems. Cyclic morphogenesis is a prerequisite for normal functioning of a living system	The controlling subsystem combines all the functional subsystems. Normal functioning of a living system is impossible without control
Neutralization principle	Dysfunctioning of the systems is neutralized by the cost of the intensity of form-building processes	Controlling processes are responsible for the elimination of dysfunctions
Instability principle	Qualitative characteristics change due to the change in the form-building processes and their algorithms	Qualitative characteristics change due to the upgrade in the controlling system
Interrelations between general organization principles		
Interrelation between structural, dynamic and regulation aspects	Development, functioning and regulation of a definitive living system are realized through the changes in its macrostructure	Development, functioning and regulation of a definitive living system are realized without any changes in its macrostructure
Interrelation between structural and dynamic aspects	Cyclic morphogenesis determines the dynamics of a macrostructure	The macrostructure is not changed in the course of functioning
Interrelation between structural and regulation aspects	Functional equivalency of modules allows the regulation of functional intensity by reducing or increasing the number of modules	Regulation involves the change in the interrelation and functioning of the system components
Distinctive features of functioning		
Interaction with environment	Passive forms of interaction prevail, such as “adaptation”, “accommodation”	Active forms of interaction prevail, such as “avoidance”, “assimilation”, “subjection”
Reaction to damages	Regeneration	Regeneration is limited, compensatory reaction is more common
Stability support	“Cold reservation” is important	“Warm reservation” is more common
Efficacy balancing	Regulation of the form-building intensity	Adequate reaction to the changing conditions
Regulation type	Passive regulation, communication “with no definite address”	Active regulation provided by the central controlling system, “addressed” communication

Table 2: Basic features of individual development for different organization types.

Feature	Modular organization	Unitary organization
Basic features of individual development		
Development program	Reuse of all morphogenetic programs during ontogenesis	Basic morphogenetic programs are not reused
Changes in the rate and extent of the structural and functional transformations	Proportional	Disproportional
Embryonic period	Poorly defined	Clearly defined
Development strategy	Development of a living system in the course of ontogenesis	Development of a living system in the course embryonic period. Functioning and improvement in the course of post-embryonic period
Integrity of development processes	Degree of integrity is considerably low; growth, aging, and terminal processes are stretched in time and space	High degree of integrity of all processes and individual development
Manifestation of the cyclic character of development	Cyclic character manifests itself on the macromorphological level: in cyclic morphogenesis and modular structure	Cyclic character reveals itself only on the anatomical level and is not expressed in the macrostructure
Tempofixation qualities	Present	Not present
Determinism of development	Development is determined to a less degree Development is more dependent on outer conditions	Development is determined to a larger degree Development is less dependent on outer conditions
Definitive living system: specific features of development		
Development strategies	Completion	Improvement
A subsystem provides for the interaction in the process of development	Form-building	Controlling
The role of morphogenetic processes	Development of the system	Maintenance of the system integrity
Boundaries of a living system	Constant shift of boundaries due to the appearance of new elements	Relatively stable boundaries
Modes of the system transformation	More important are transformation caused by changes in the number of elements	More important are transformation caused by changes in relations between the elements

The modules in modular objects are usually *unified*, equivalent and interchangeable as a result of a fuzzy structural and functional differentiation and indistinct delimitation of morphofunctional subsystems at the macromorphological level. For example: fungi have no differentiated morphofunctional subsystem within a vegetative body. Their modules are *polyfunctional* and capable of performing all the basic functions of the system. In the case of a distinct morphological differentiation of a body (higher plants, colonial animals), modules are also polyfunctional, as they include the elements of different morphofunctional subsystems, for example: leaves and stems of plants, zooids and communication systems of colonial animals. Leaves, stems and shoots of plants are often called organs, but these structures are unlike the organs of unitary animals. It is accepted to apply the term "organ" to more or less solitary part of an organism performing a certain function (SCHMALHAUSEN 1947). "Apparently, organs of a plant correspond to the systems of tissues running through the whole plant body and providing not only for the life support, but also for the interconnection of the parts and the integrity of the organism" (SHAFRANOVA 1980: 439).

Dynamic aspect

Normal functioning of a living organism, as well as its consistency and integrity are maintained by constant growth and decomposition of its elements (BEKLEMISHEV 1964a, 1994). In hierarchical multi-level systems these processes take place on different structural levels (molecular, cellular, tissue and organismic). The level of the growing and decomposing elements differs as well.

Reparation processes in multi-level unitary objects are carried out on the molecular or cellular levels (formation of new blood elements, epithelial and epidermal cells). The renewed structures can be multi-cellular, but such examples are rare (different epidermal structures of vertebrates, such as feathers and horns).

New growth and decomposition processes in modular objects take place on the macro-morphological level, and the newly formed elements contain all or almost all morpho-functional subsystems which are typical for the object. In many cases normal functioning of an organism involves regular discharge from some parts of the body (leaves, shoots, zooids). These parts may be of a considerable size and have a complex structure. The modular objects with a well-balanced decomposition and new growth can be considered as "hyperdynamic" living systems.

If growing of a modular object's body takes an appreciable length of time, it is possible to discern the shift of its centers – the areas of a maximum physiological activity. As a rule, such centers correspond to meristematic zones (apexes, buds of growing zooids, cambial zones with adjacent active areas of the xylem and phloem). These areas usually shift in the centrifugal direction. In the development cycle of the structural units it is often possible to distinguish the phase of a second-order activity with a narrower range of functions (SEREBRYAKOVA 1971). For plant shoots this phase starts after abscission of the apexes and leaves (SEREBRYAKOVA 1971; BOLOGOVA 1989). A considerable difference in the physiologic activity can be observed, if we compare conducting and non-conducting levels of the xylem and phloem of woody plants.

The most important properties of the system are stability, effectiveness, and economy (NOVOSELTSEV 1978). A special research is needed to describe how these properties are ensured in the objects of different organization types. In many cases, the stability of modular systems is achieved through "*cold* reservation" (STAROSTIN 1966, 1967). This mechanism is much better studied for plants (STAROSTIN 1966, 1967; GROZDINSKIY 1974, 1983). "Cold reserves" can be found on different structural levels of plants (deposits of assimilators in the storing organs, resting centers in meristems (IVANOV 1974), dormant buds). The stored nutritive materials have been discovered in the hypertrophied gastrodermis of hydroids (MARFENIN 1993a: 35). Some ascidiata have analog dormant buds (MARFENIN 1993a: 147).

Physiological mechanisms providing the effectiveness of functional processes in unitary organisms have been studied much better (ANOKHIN 1975, 1978, 1980; UGOLEV 1985, 1987). For modular objects quantitative analysis of productivity is usually performed, sometimes the dynamics and functioning is also considered (BOLOGOVA 1989). YURTSEV (1986) suggested an interesting approach that allows the functional interpretation of major production strategies and phytocoenotypes.

Passive forms of interacting with environment are predominant for modular objects (STAROSTIN 1966, 1967) (Table 1). Such forms of adjusting to adverse conditions as anabiosis and cryptobiosis are typical for many groups of spore plants as well as for modular objects in general. Some hydroids outlive the seasonal diapause without hydrants, in a passive form (MARFENIN 1993a: 35). Vitality is often reduced under adverse conditions (quasi-senile condition of plants) (SMIRNOVA et al. 1984), starving specimens of hydroids (MARFENIN 1993a: 117).

Unlike unitary objects, which are moving actively, modular objects mostly have a static form.

Regulation aspect

Apparently, A. BRAUN was the first to suggest that the growing apex of a plant has the "leading" role (BRAUN 1853). He compared the apex to the head of an animal. At present, apexes are seen as the main coordination centers influencing morphogenetic processes of a whole plant (KEFELI 1984, 1994; ROSTOVTSEVA 1984; BATYGIN 1986; POLEVOY 1989; POLEVOY & SALAMATOVA 1991). In recent studies the role of apexes in synthesis and hormone redistribution was asserted, and it has been shown that hormone interaction in the main centers of a shoot and a root serves as the primary endogenous mechanism regulating the growth and morphogenesis of a plant (POLEVOY 1989).

Different production strategies are dictated by the genetically determined types of regulative mechanisms with a different correlation between intensity and stability of production processes (YURTSEV 1986). All the major phytocoenotypes and production strategies imply certain dynamics in the intensity and duration of growth processes.

For any phytocoenotype the reaction to stresses and damages is directly or indirectly connected to the change in form-building activity. Violents (competitors) and explorents (ruderals) react to stress by an active growth (etiolation effect in the insufficient light, regeneration of damaged shoots and roots) (YURTSEV 1986). The growth of patients is affected to a less degree, but some parameters of their physiological processes can alter (photosynthesis, respiration). A heavy impact may cause a switch to a dormant state, but assimilation organs are preserved. This switch results from the stop in growth processes.

Preservation reactions to a serious damage of a plant or a colony of animals are aimed at the *regeneration* (YUSUFOV 1972, 1982; MARFENIN 1993a).

Various types of correlation are the exterior expressions of the inner mechanisms of interaction between structural elements of different levels. Balanced development of the different elements (correlations between the root and the leaf (KAZARYAN 1969)), correlations between a rhizocormus (rootshoot) with different development variants (BOLOGOVA 1989) is ensured by the regulation of form-building intensity. Our conclusion, that the form-building subsystem plays an important role in regulation, is supported by the information about proportionality of the colony structure of colonial hydroids (MARFENIN 1993a,b) and the growth pattern of different areas of mycelium. Apparently, the form-building system performs the function of coordination on the level of a whole colony of colonial animals with under-developed nervous system.

Thus, the interaction of subsystems in modular objects is provided by the form-building subsystem, and it can be considered analog to the controlling subsystem of unitary objects.

Basic principles of functional organization and interconnection between its aspects

The fundamental principles of organization summarized by M. I. SETROV (1971a,b, 1972) have one specific characteristic common for all modular objects: the form-building subsystem plays a special role in *development* and control (Table 1). This role imparts a *functional* character to form-building processes. Cyclic morphogenesis becomes both a prerequisite and a means of normal functioning (Table 1).

The form-building processes in unitary objects have a purely reparation character and do not affect the *macromorphological* level. All functional subsystems are joined together by the controlling system which provides the integrity and development of the system.

Before formulating the general rules of modular organization, it is worth mentioning the *specific interrelations* between its structure, dynamics and regulation. Evidently, the essence of these interrelations can be summarized as follows: the development, functioning and regulation of a definitive living system are performed *by changes in its macrostructure* (Table 1).

The dynamic character of the macrostructure accounts for *the constant shift of boundaries* in a definitive living system, the instability of its composition (Table 1), though the structural stability of modular objects is ensured by the stability of the growth algorithm. This is also one of the qualitative characteristics of modular organization. That is why studies on the structure of modular objects should always include its dynamical and functional aspect (BOLOGOVA 1989).

Functioning and regulation of definitive unitary objects do not result in the change of their macrostructure (Table 1).

Similarities in functional organization of modular objects and populations

"The specific character of this or that class of systems is specified by the connection between elements in the system, their organization and relation to adjacent (hierarchical) structural levels" (SETROV 1972: 114). From this point of view it would be interesting to compare general organization principles of modular objects and populations.

Modular objects and organisms are capable of reproducing their elements repeatedly throughout the lifetime. The reproduction is performed *within the system*. In 1866, K. E. VON BAER defined reproduction as "growing beyond the limits of one's individuality" (IVANOVA-KAZAS 1977: 4). Reproduction or "growth" of modular objects and populations takes place within the system or "individuality", though the integrity of a population is much lower than that of an organism. Constant formation of new elements maintains not only the integrity of the population, but also contributes to its *development*. The growth of unitary objects takes place "beyond the limits of their individuality", in accordance with BAER's definition.

The properties of elements in modular organisms and populations are similar. The elements are *homonomous*, functionally *equal*, *interchangeable*, and relatively *autonomous*. In both the systems regulation is performed by changing the rate of formation and decreasing or increasing the number of new elements (the intensity of form-building processes and reproduction, correspondingly).

Development, functioning and regulation of modular objects and populations imply *changes* in their *structure* and composition. New elements and new relations are formed in the course of development and functioning.

Unlike modular objects, unitary organisms are systems of *strong* linkages established between *heteronomous*, *unique*, and *irreplaceable* elements.

Thus, the basic features and organization principles of modular objects are similar to population systems. It is not surprising that many researchers tried to represent a plant as a colony or a metapopulation (WHITE 1979), and to apply "demographic" method to characterize quantitative correlations between structural elements of different classes (BOLOGOVA 1989: 22).

The fact that structural elements of a modular object are in *competitive* relations (BOLOGOVA 1989) confirms our hypothesis. Using *Dactylis glomerata* as an example, it was ascertained that structural elements of its tussock are more likely to perish at the early stages of development.

These objects, which are capable of forming clones, are even more similar to populations. In this case there is no physical connection between the parts of a modular organism. Cloning is common for plants and fungi. In the colonies of hydroid polyps the elements can isolate themselves if the central part of the colony is ruined (MARFENIN 1933a: 43).

Individual development of modular and unitary objects

Specific features

Ontogenesis of living objects approached as an organized process can be roughly subdivided into three main aspects: structural, dynamic and regulative.

Structural aspect

The structure of the process is determined by its distribution in time: the number and length of periods and the integrity of the periods and the whole process.

During embryonic period unitary objects often undergo different topological transformations: migration of cell elements, local necrosis, and complex transformations of the whole organization (KNORRE 1971; KOROTKOVA 1968, 1979; ZAVARZIN, 1985; PRESNOV & ISAEVA 1985; BELOUSOV 1979, 1993). These processes lead to the development of a definitive system with a certain structure and functional organization. Having compared ontogenesis of plants and animals, IHLENFELDT (1971) came to the conclusion that "ontogenesis of animals is a "one-time" process, and it is not surprising that many zoologists do not consider the existence of a grown organism as ontogenesis and combine ontogenesis studies with embryology" (quoted after SEREBRYAKOVA 1983: 580–581).

In the course of post-embryonic period the rate of transformations in unitary objects slows down. During this period the organism is functioning (Table 2). Most transformations are of quantitative character. Qualitative transformations are connected with reproduction and, later, with aging. Aging can be considered as a characteristic feature of development. "Programmed death" (KOGAN 1977; ADO 1980) resolves the contradiction between self-preservation of an individual and preservation of a species. A living system with a *well-developed* controlling subsystem (nervous system) is capable of self-improvement by increasing the efficacy of the subsystem (Table 2).

Thus, the difference in development and in the rate and degree of transformations permits us to break the ontogenesis of most unitary objects into two periods: embryonic and post-embryonic (Table 2).

Modular objects have cyclic morphogenesis and constant formation, and their development continues through the *whole ontogenesis* (Table 2). Individual development in this case is monodirectional. Cyclic morphogenesis dictates *proportional* character of the rate and intensity of transformations (Table 2), which increase as the growth centers enlarge. Because of all these factors it is difficult to define embryonic period in the strict sense. For example: plant embryology, developed mostly for angiosperms, usually includes the formation of spores, gametophyte, fertilization and the early stages of development of sporophytes (TOKIN 1987; SLADKOV & GREVTSOVA 1991). The later stages are excluded from embryology because of the seed formation. The earlier stages of development of higher spore plants are even less distinct.

Compared to plants, the embryonic period of modular animals sticks out more clearly. At the same time, modular animals have a relatively simple embryogenesis and they continue to form new zooids, therefore the rate and intensity of transformations in modular animals do not vary much. The combination of all these factors permits the conclusion that embryonic period of modular animals is less distinct than that of unitary objects.

Major development processes (growth, morphogenesis, aging, and the terminal process) are stretched in time, and there is no strict demarcation line between them. The developmental stages can be rearranged; time-reversible states are also possible, such as quasi-senility (SMIRNOV 1984). Terminal processes can acquire a transient character. With some plants it is almost impossible to trace the final stages of ontogenesis.

Dynamic aspect

Stability of any phenomenon is ensured by dynamic processes of a closed and cyclic character (SETROV 1972: 80). Modular objects with a morphologically separated body have a complex hierarchy of morphogenetic cycles (SHAFRANOVA 1990). Their ontogenesis acquires a *cyclic* character and consists of repeated "partial" ontogeneses of a different scale.

The *cyclic* character of functioning and development of modular objects is expressed on the *macromorphological* level (Table 2). The structural and dynamic aspects of modular objects are closely connected, so it is difficult to study them separately. Such terms as "dynamic macrostructure", "dynamic morphology" (SHAFRANOVA 1990; SATTLER 1992), and "ontomorphogenesis" convey this interrelation.

The dynamics in the development of a macrostructure of modular objects can be illustrated by *tempofixation*. This phenomenon is evident in plants (SHAFRANOVA 1990), and is manifested on different structural levels: anatomical and macromorphological. With colonial animals tempofixation is found in objects with a massive skeleton, for example: in corals. The growth of a stalk in the course of the secondary development of hydrants, described by MARFENIN (1993a: 115), is another example of tempofixation.

During postembryonic development the macrostructure of unitary objects is not changed much, and the cyclic character of functioning is observed only on the *anatomical level* (Table 2).

Growth and extinction processes are of *local* character in modular objects. Inaequipermanence of the system elements and their different physiological quality make "local" aging and rejuvenation possible. As a consequence, major development processes are often isolated. Physiological heterogeneity of the different parts of modular objects is better represented in plants. With colonial animals, Marfenin has described the depression zone in the center of a colony where zooids or sometimes a coenosarcs are dissolved (Marfenin 1993a: 43).

Regulation aspect

Development is regulated by the subsystems of different levels (Schmalhausen 1935, 1961, 1964, 1968; Svetlov 1978a,b; Lodkina 1983; Polevoy 1989). The most important regulator is the genome. In contrast to unitary objects, the development of modular objects involves a *reuse* of morphogenetic programs in their ontogenesis (Table 2).

The development of modular objects is determined to a less degree than the development of unitary objects. *Low determinism* of development manifests itself in the undetermined number of modules, morphogenetic cycles, duration of some phases and stages of ontogenesis and individual development (Table 2). One of the most conspicuous manifestations of low determinism is *polyvariance of ontogenesis*. At the same time, polyvariant ontogenesis is indicative of low autonomy of development, of its dependence on outer conditions. In a certain sense, polyvariant ontogenesis can be considered analog to animal behavior (Arber 1950: 3).

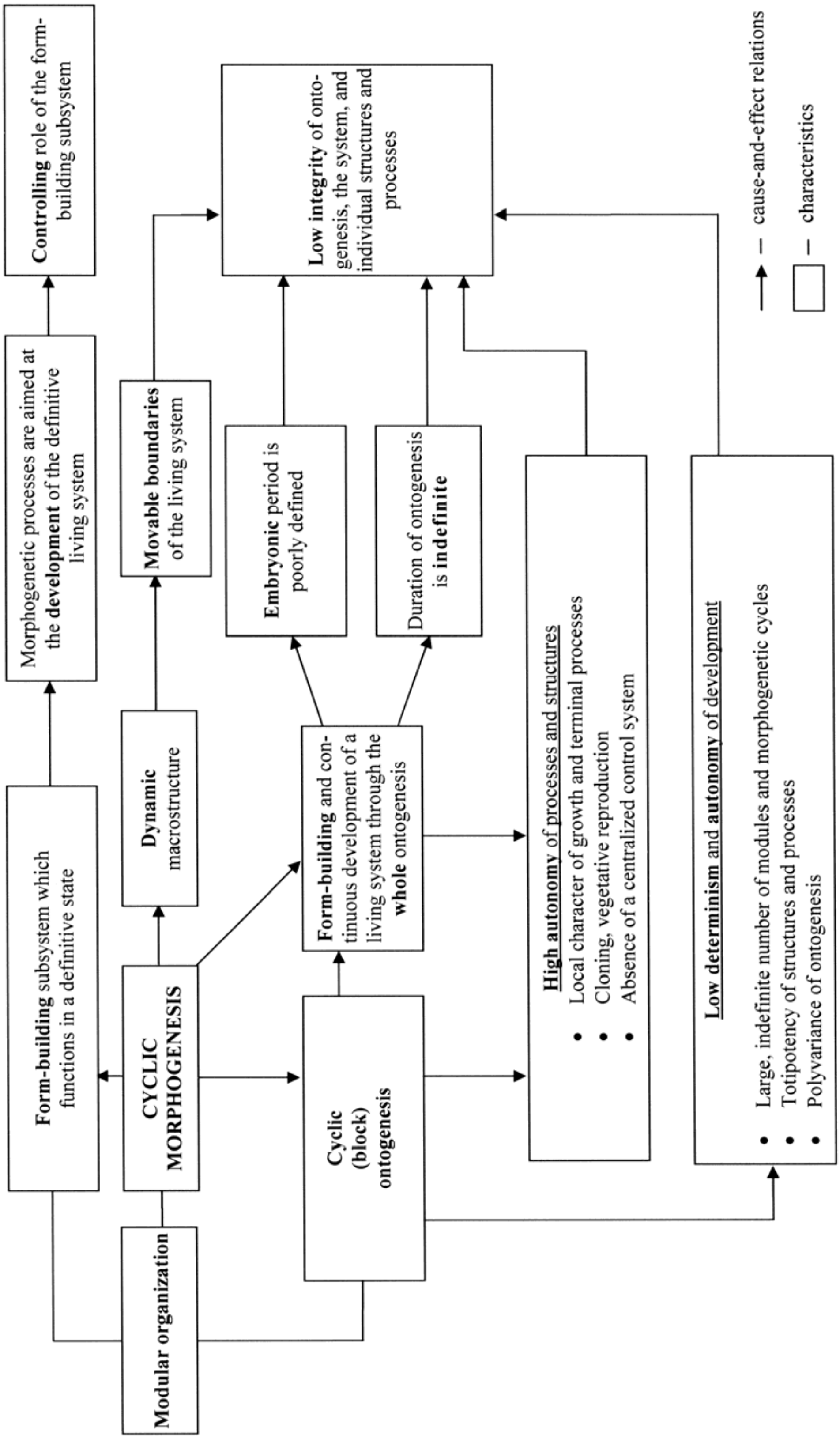
The concept "polyvariance of ontogenesis" is worked out in detail for higher plants; its major types have been described (Zhukova 1986; Nukhimovsky 1997, 2002). Some manifestations of polyvariant ontogenesis can also be found in other groups of modular objects. For example: colonial hydrants can build different variants of colonies, depending on the type and current velocity of the substrate or the type of forage (Marfenin 1993a). Different organization types (yeast-like or mycelium forms) have been described for fungi depending on the deep or surface culture (Cherepanova 1981; Bilai 1989). According to our observations, some species of lichens with a composite thallus (for example: *Cladonia gracilis*) have two major organization types: the first type involves long-term functioning of the primary thallus and podetia, while the second one results in a quick disintegration of the primary thallus and intensive changing of elementary podetia (Ivanova & Notov 2005). The further development of the concept "polyvariance of ontogenesis" and periodization of ontogenesis for different groups of modular objects is of topical importance.

The connection between main functional characteristics and individual development

Cyclic morphogenesis – the most important functional characteristic of modular objects – determines the qualitative specificity of their individual development (Diagram 1). The qualitative specificity of modular objects can be defined as follows: in a definitive state they represent life systems with *movable boundaries* and their ontogeneses have a *cyclic character* (Diagram 1). The boundaries of the system change through its life time due to appearance of new elements and new relations between them. The instability of the system's boundaries results in its low integrity. The whole development process is also characterized by *low integrity* manifested in poor delimitation of the stages, indefinite duration of the separate stages and the whole ontogenesis, high autonomy of some processes, low determinism and high autonomy of development (Diagram 1).

Diagram 1

The connection between main functional characteristics and individual development in modular objects



Modular organization and other aspects of studying living objects

Cyclic morphogenesis determines the major features of structure and functioning of modular objects – *plurality, repetition and equality* of modules (Diagram 2). These features, in their turn, are responsible for the specific character of the intrasystem and external relations, which is revealed in the special coenotic role and structural evolution of modular objects (Diagram 2).

Synecological aspect

Because of their constant growth, immobile modular objects divide their environment, transform it, and enlarge the number of ecological niches (MARFENIN 1993a: 130–135). Some modular objects can have several centers of influence on the environment. This feature is more pronounced in objects representing polycentric life forms. This characteristic accounts for the *coenotic* role played by modular objects (Diagram 2). The complexity and diversity of biocoenosis depends on the structure and composition of phytocoenosis formed by modular plants. With modular animals the same role is played by corals.

Evolutionary aspect

The plurality, equality, relatively simple structure and morphogenesis of modules determine the character of structural transformations (Diagram 2). With the major modes of transformation, described by MAMKAEV (1991, 1996), special role is played by the modes which involve the change in the *number* of elements: "*assembling*" and "*addition of elements*".

Even the most integral structures of higher plants (ovules, hypanthiums, leaves, macrophylls, seed scales) are formed as a result of integration processes (KRASILOV 1970, 1989; MEYEN 1977, 1982; TAKHTADJYAN 1983; KUSNETZOVA 1986).

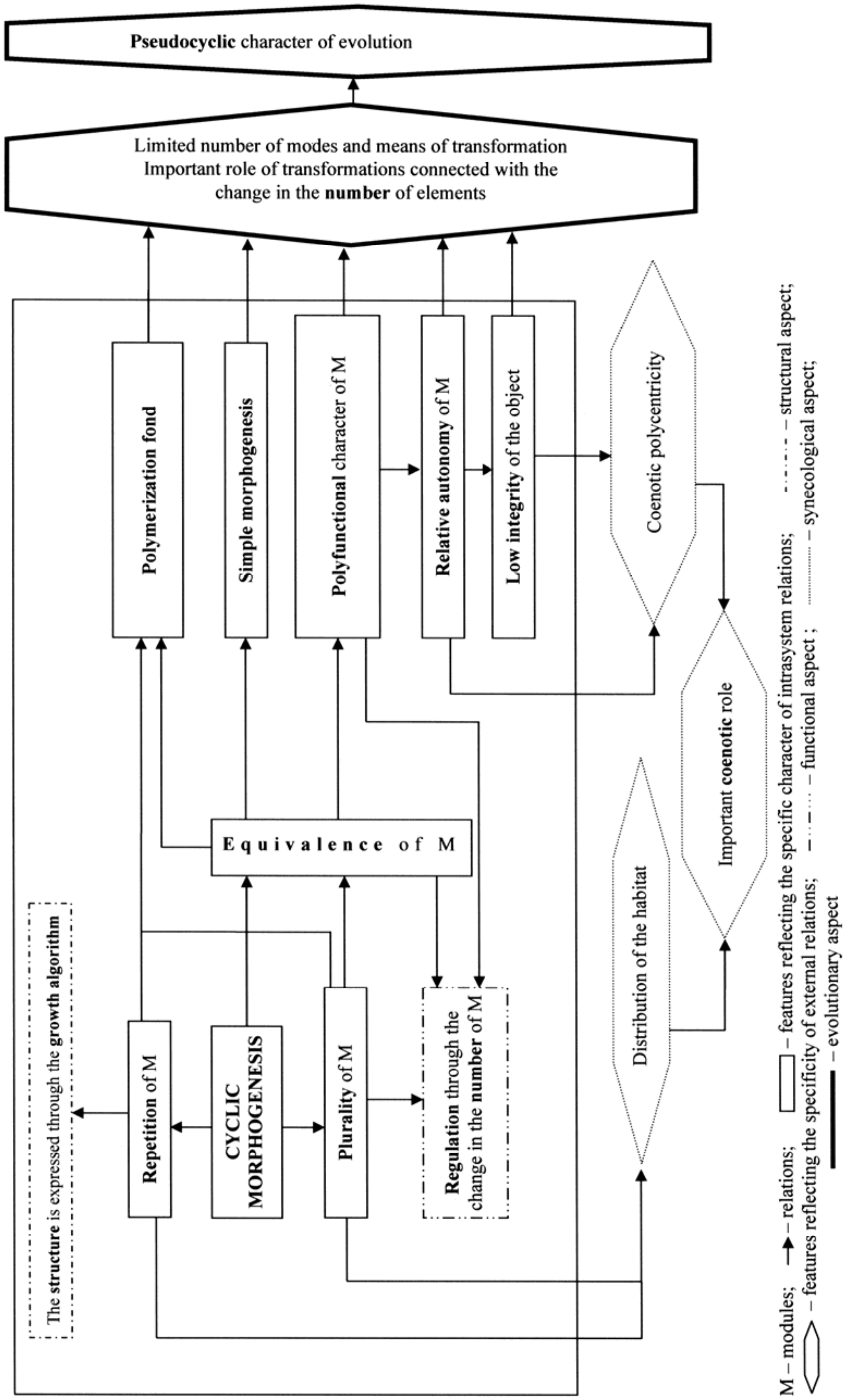
Integration processes have been described for different animal groups. For example: merging of hydrants results in the formation of polysyphon stems (MARFENIN 1977, 1988, 1993a). Merging of zooids and formation of the "secondary single (unitary)" forms are common for colonial pearlworts, corals, tabulata, and tunicata (BEKLEMISHEV 1964b; PREOBRAZHENSKIY 1982; NAUMOV et al. 1987; ROMANOV 1989). In some cases the merging of zooids leads to the formation of a common mouth. For example: colonial madrepore corals have a tendency for merging polyps. Leptoria and Diploria have all the polyps merged together (NAUMOV et al. 1987). Their colonies are shaped like a semi-sphere with apertures formed by adhering mouths of polyps. Obviously, flat lamellate forms (*Leptogorgia petechizans – Gorgia flabellatum – Phyllogorgia dilatata*) originate from the flattening and merging of the elements of branchy forms. With fungi merging of hyphae results in the formation of rhizomorphes (CHEREPANOVA 1981; BILAY 1989).

The periodic and cyclic character of integration processes is described in the researches on polymerization and oligomerization (DOGGEL 1954; ZAMORSKIY 1971, 1980; KHOKHRYAKOV 1974, 1975; MAMKAEV 1977). The concept of pseudocycles is based on the same presumptions (KUSNETZOVA 1985, 1986, 1992).

The periodic, cyclic character of "assembling" can be demonstrated for plants by the example of the group "system of telomes – macrophyll – phyllomorphous branches of different structure". The repetition of such "assemblages" results in the similarity of non-homologous structures (*pseudocyclic* similarity). The forms possessing such a similarity can be grouped into pseudocyclic

Diagram 2

Some peculiarities of modular objects reflecting the specific character of intrasystem and external relations



series characterized by the repetition of the similar non-homologous forms bound together by gradual transition (KUSNETZOVA 1986, 1992). Zoological objects are studied insufficiently from the point of view of pseudocycles, but the data available on unitary forms and on the merge of zooids suggest that pseudocyclic transformations are prevalent in the evolution of modular objects.

Pseudocyclic character of evolution is responsible for the *instability of boundaries of morphofunctional subsystems*. There are numerous examples of the shift of the subsystem boundaries within a shoot (inclusion of axial elements or generative and vegetative areas into the "functional" phyllome (phyllomorphous branches, inclusion of the vegetative area into generative structures – the covering of an ovule, inflorescence axes in the syconium, and inclusion of persisting elements into inflorescence). Repeated merging and inclusion of the subsystem elements account for the *complex* transformations which involve changes in the number and quality of elements and the character of relations between them. The complexity of transformation makes it difficult to analyze individual aspects of transformation (URMANTSEV 1978, 1980, 1988; MAMKAEV 1997). The change in the number of elements leads to the change in their quality. At the same time, the relations between the elements often remain unchanged (for example: axillary position of buds and shoots of gemmaxylem plants in the process of transformation of their vegetative sphere (formation of phyllomorphous shoots) and generative sphere (change of the border between the perennial shoot system and the florescence in groups where subshrubs and herbs are represented).

The inequality of main transformation modes and their interdependence suggest low integrity of the system. The boundaries of the systems under study are poorly defined, and the relations between the elements are weak. The changes in the number of elements are also indicative of the low integrity of the system. In the integrated morphofunctional systems quantitative changes are hindered by strong correlations (MAMKAEV 1991).

Modular organization as a model object in biology

The comparison of modular and unitary objects allows us not only define their specific features, but also establish analogies between the two major groups. These analogies are:

- growth algorithm of modular objects – structure of unitary object,
- form-building subsystem – controlling subsystem,
- phytocoenotypes – temperament types (YURTSEV 1983),
- ontogenesis of modular objects – behavior of unitary objects,
- organism of modular objects – population of unitary objects,
- the shift of activity centers in modular objects – active movement of unitary objects.

These analogies reflect the general organization principles and transformation trends of living systems. These principles and trends can be manifested in a different way depending on the organization type. From this point of view, modular organization can be an interesting model object.

Strong integration of morphogenetic and ontogenetic processes is one of the general tendencies in the evolution of all living objects (YUSUFOV 1988). This tendency being realized, modular objects can develop some features typical for unitary organization, such as delimitation of development and functioning stages or high integrity of the terminal process. This tendency is more explicit for monocarpic plants. In modular organization high integrity can be achieved on the level of individual structures: buds, leaves, flowers, flower stalks (for plants), and zooids (for animals). In this case the similarity between modular and unitary objects is extended due to stabilization of the number of elements (flowers).

The similarity between some features of modular and unitary objects can be of formal character. For example: the number of structural units and the system boundaries of modular objects can become relatively stable, if the processes of form-building and dying are balanced (some corms, vegetatively movable). The functional analysis of such objects and typical unitary organisms gives the insight into the nature of these similarities.

Modular organization can undergo even more drastic changes. For example, a sharp increase in the rate of vegetative reproduction combined with reduction processes can result in the total rearrangement of the typical modular structure (some representatives of Lemnaceae). In this case physical connection between the modules is so short-term, and the shoot structure differs so much from the typical one, that we can call it a "secondary-unitary" object. Such objects have much in common with populations.

Evolution of any organization involves an increase in the level and degree of organization. If this tendency is realized, the correlation between stability and functional instability is also changed (SETROV 1971b, 1972).

Unitary objects do not have such a flexible ontogenesis and labile structure as modular objects. In this respect lichens and moss-like plants deserve special attention. Some of representatives of these two groups have bodies differentiated on the macromorphological level and a complex system of structural units (*Cladonia, Climacium dendroides*), but their structural and functional differentiation is determined to less degree than that of vascular plants, though their architectural models and complexity of structures are quite comparable. For example: *Climacium dendroides* have a rigidly determined architectural model (compared to other moss-like species), but under different environmental conditions all the types of structural units typical for this plant are formed within its "crown" (NOTOV 2004). The similar architectural models found in modular objects of different levels make it possible to establish the correlation between structural and functional flexibility and the level of organization. The functional and dynamic analysis of macrostructure (BOLOGOVA 1989; MARFENIN 1933a) can be very helpful for further research in this way.

Conclusion

The functional analysis of organization allows us to combine different aspects of organization. Functional specificity is responsible for the peculiarities of the individual development, ecology, and evolution of modular objects. Thus, functional approach makes it possible to interpret different aspect of modular objects from this point of view.

The primary difference between modular and unitary organization can be summarized as follows: development, functioning and regulation processes in a modular object are connected with changes in its macrostructure. The dynamic character of the macrostructure is responsible for the instability of the system boundaries and close interconnection between the major aspects of the organization. The aspects are so tightly connected that it is difficult to divide them and study separately.

The description of the macromorphological structure should be based on the analysis of its dynamics and functioning. Thus, there is a need in the development of theoretical morphology of modular objects, so that general problems can be solved with the help of specific methods.

The objects with modular organization have many features in common with the systems of populations, especially in their functioning and development.

The analysis of functioning, individual development, and structural evolution reveal the lower integrity of modular objects compared to unitary objects.

Numerous analogies revealed by the comparative analysis of modular and unitary systems permit us to use modular organization as an ideal model object to elucidate the general tendencies in the transformation of both organization types.

Acknowledgements

The author is extremely grateful to his mentor Tatiana V. Kusnetzova, Prof. Alexander K. Timonin, and Yulia Lissina who made the publication of this article possible. This investigation was supported by the grant of RFBR (№ 98-04-48469).

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