

Chapter 5

General Evolutionary Regularities of Organic and Social Life

Valeria I. Mikhalevich

Abstract The main evolutionary regularities were firstly and more fully studied in biological sciences. An important contribution to the subject was made by the Russian evolutionary school, elaborating the evolutionary ideas mostly on multicellular organisms. Protista (mainly Infusoria) in these investigations were only slightly touched upon. The present study represents the results of a comparative morphological analysis of the vast protistan group Foraminifera, showing the manifestation of the evolutionary regularities at the unicellular level. Research concentrated on the major regularities—polymerization, differentiation, and integration—representing the mainstream of evolutionary development and permitting the structures to achieve a new higher level of organization. The phenomenon of aromorphoses is partly touched upon. It is also shown that these processes have a general character and can be applied to the social level of life as well.

5.1 Introduction

The investigation of the regularities of evolutionary development began with the classic works of Cuvier (1801), Lamarck (1804), and Darwin (1859), and a significant contribution to the study of evolutionary mechanisms was made by the scientists of the Russian school (Berg 1922; Severtzov 1925, 1939; Schmalchhausen 1939, 1946; Dogiel 1929, 1954; Beklemishev 1964; Golubowski 1994; and others) and multiple recent studies. All of them were based mainly on biological objects and predominantly on multicellular organisms.

V.I. Mikhalevich
Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1,
St. Petersburg 199134, Russia
mikha@JS1238.spb.edu

P. Pontarotti (ed.), *Evolutionary Biology from Concept to Application*,
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The investigation of the evolutionary regularities of unicellular organisms was difficult because of the minute sizes of these objects and the scarcely lack of structural morphological characters.

Foraminifera—the vast group of protists—represents in this regard one of a lucky exceptions owing to the variability and complexity of their skeletons, which is unusual at the unicellular level. The abundant occurrence of their agglutinated and calcareous shells in the geological strata since the Cambrian also provides an opportunity to study their evolutionary development through time. Foraminifera are sea animals that have existed to the present and whose soft cell is enclosed by an agglutinated or calcareous (rarely tectinous) shell. The animals communicate with the environment through an opening in the shell—their aperture—protruding and spreading the cytoplasmic reticulopodia (Figs. 5.1 and 5.2). The cytoplasm of the living animals owes its color to the different symbiotic algae.

In Fig. 5.2 there are shown the main phyletic lines of this group: classes Astrorhizata, Spirillinata, Nodosariata, Miliolata, and Rotaliata (according to the classification proposed by Mikhalevich 1980, 1981, 1992, 1999, 2000, 2004 2005). It was supposed that their early representatives lacking a hard test existed much earlier (Mikhalevich 1981, 2000; Mikhalevich and Debenay 2001). Molecular data of Pawlowski et al. (2003) have clocked that the early foraminiferal evolution occurred between 690 and 1,150 million years ago. These data are in agreement with the data of other authors (Hengeveld and Fedonkin 2004) on the origin of the early eukaryotes in the Neoproterozoic. Nevertheless their skeletons, as well as the skeletons of the other animal groups, have been well preserved since the Cambrian. Many of the representatives of each of the classes shown in Fig. 5.2 are still living in the seas. Class Rotaliata has the most recent origin (Mesozoic, though its earlier

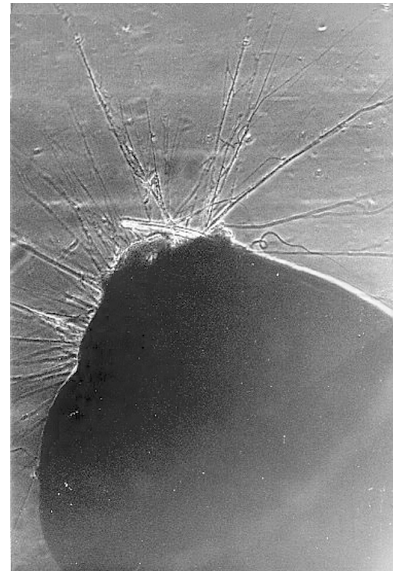


Fig. 5.1 Apertural part of the living *Massilina secans* (d'Orbigny), 1826, littoral Ile d'Yeu, Biscay Bay, 1998, with extruded reticulopodia ($\times 50$)

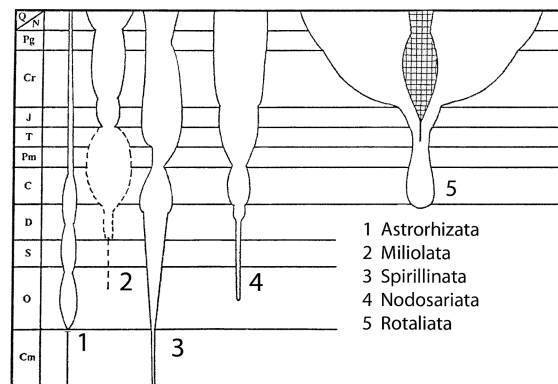


Fig. 5.2 The main phyletic foraminiferal lines (classes) according to the classification of Mikhalevich (1992) (scheme, not to scale) (the *dotted line* outlines the previous heterogenous taxon Textulariina of Loeblich and Trappan 1987). Note the unilocular shells at the beginning of Nodosariata and Miliolata lines, pseudo-two-chambered shells with the long tubular second chamber at the beginning of Spirillinata and Miliolata lines, and supermultichambered shells at the end of Miliolata and Rotaliata lines

more primitive representatives are known from the Carbonaceous), Nodosariata and Miliolata are known from the Ordovic, and Spirillinata are known from the Cambrian. Astrorhizata, which are the more primitive and always unilocular forms, existed in the Pre-Cambrian (Fig. 5.3).

After the first study of d'Orbigny, in 1826, foraminiferal classification was based on the features of the skeletons of Foraminifera. From Schultze (1854) to the most widely used classification of Loeblich and Tappan (1964, 1987), predominant significance was given to the peculiarities of the composition of the shell wall (agglutinated with sand particles attached or calcareously secreted) and its structure. The possibilities presented by the introduction of electronic microscopy permitting ultrastructural studies strongly strengthened such an approach. As a result, many of the previous foraminiferal taxonomic groups were divided into a number of different ones which were placed in the remote phyletic lines in spite of their nearly full shell structure isomorphism. The isomorphic forms were regarded as the consequence of the convergent evolutionary development. Thus, all the agglutinated forms, including all the existing morphotypes of the foraminiferal shell, were united in one taxon—Textulariina (Fig. 5.2). Spirillinata and Rotaliata lines were split into several groups of equally high taxonomic rank.

After the thorough comparative morphological analysis of all the main foraminiferal taxa, a new classification scheme (Fig. 5.2) was proposed (Mikhalevich 1992, 1998, 1999, 2000), based mainly on the morphological features of the foraminiferal shell regarding the composition and ultrastructure of the shell wall as having important but subordinate meaning. Under such an approach the agglutinated and calcareous isomorphs showing profound similarity in their shell and apertural structures and similar tendencies in their ontogenetic and phylogenetic development were placed within one phyletic line (class), their resemblance being



Fig. 5.3 The development of different foraminiferal classes in geological history (in Miliolata, Fusulinoida are included, *dotted line*; in Rotaliata, planktonic Globigerinana are shown *checked*). (Modified after Mikhalevich 2000)

considered a result of the close relationship rather than of convergence (Mikhalevich 2000, 2004). The agglutinated forms may represent the earlier phylogenetic stages of the development of their calcareous isomorphs or their sister groups. Some of the new data of the foraminiferal cell, especially those of the character of the nuclear apparatus, also support the separating of these five classes. These cytological characters were used as the taxonomic features of the classes for the first time. Further discussion in this chapter is based on this new classification scheme which in its four lines (Astrorhizata, Miliolata, Spirillinata, Rotaliata) was later supported by the molecular data of the Pawlowski school (Pawlowski et al. 2003) (data on Nodosariata are still absent).

Each of the five classes could be specified in terms of its special morphological features, such as plan of the structure of the shell connected with the functioning

of its parts, predominant modes of coiling, characteristic form of their chambers, position of the aperture and its outer and especially inner apertural structures, and development of additional systems (additional apertures, different types of integrative systems).

5.2 Processes of Polymerization in Foraminiferal Development

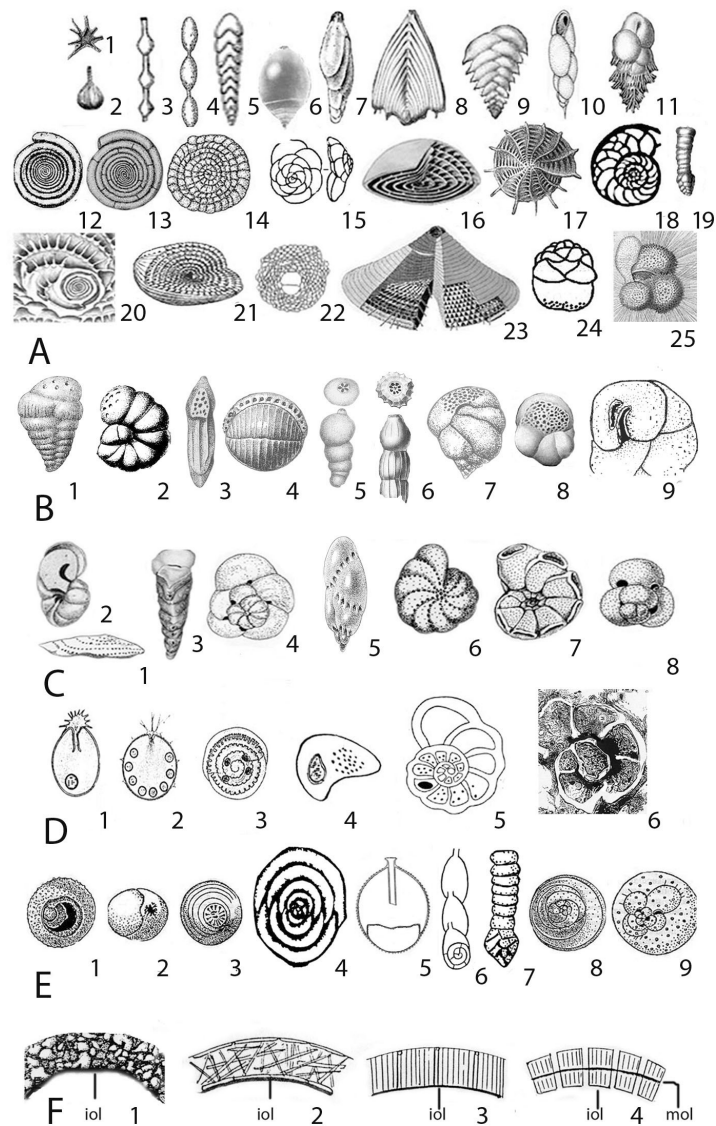
The main evolutionary processes having some specific features in these different classes (Fig. 5.2) occurred independently and in parallel in each of them during the geological time. Thus, the majority of the classes began their development from the unilocular (Astrorhizata, Nodosariata, Miliolata) or pseudo-two-chambered (sub-spherical proloculus followed by a long tubular second chamber—Miliolata, Spirillinata) forms (Fig. 5.2). Astrorhizata, including forms with only an agglutinated or tectinous shell wall (subclass Lagynana), did not get beyond the unilocular level of organization, being unilocular throughout. In the rest of the classes evolutionary development resulted in the creation of multichambered shells at the ends of their evolutionary branches (Spirillinata, Nodosariata, and Miliolata) or from the very beginning of their development (Rotaliata) (Fig. 5.2). In the more primitive multichambered forms there are three to seven chambers (Fig. 5.4, group A, nos. 3, 4); more usually there are 25–30 (Fig. 5.4, group A, nos. 6–15). In the two phyletic lines—in Rotaliata and Miliolata (Fig. 5.2), supermultichambered shells are known, where there may be up to thousands of chambers (Fig. 5.4, group A, nos. 16, 21–23).

What were the main ways and the main regularities of foraminiferal development that resulted in such variable and complex forms? The first stage of foraminiferal evolution manifested in the transition from the unilocular to the multichambered and even supermultichambered shell was the process of polymerization (the increase in similar homologous formations in the organism). Polymerization could take place in all living organisms—for instance, in the Metazoa cells are polymerized. The peculiarity of the Foraminifera as well as other Protista is that this process occurs within a single cell. In such tiny animals, pure in their structural features, polymerization is the basic primary process permitting further development—the second stage of the evolutionary process—the process of differentiation, and providing the base for it.

Some other skeletal structures in Foraminifera were the consequence of the processes of polymerization. Thus, the apertural openings of the main aperture of the shell could also be polymerized in the different phyletic lines of Foraminifera (Fig. 5.2, group B, nos. 1–9). And above the main aperture in some advanced foraminiferal genera additional (supplementary) apertures appeared (Fig. 5.4, group C, nos. 1–8). Depending on their disposition in the shell they are called sutural, umbilical, or peripheral supplementary apertures. Supplementary apertures are widely represented in the class Spirillinata and especially in Rotaliata; in Miliolata and Nodosariata only one or two genera having supplementary apertures are known. Supplementary apertures represent an example of multiplication not only of the apertural openings but also of the number of apertural systems and at the same time

of the differentiation of the apertural system into the main and supplementary ones. The multiplication of all types of apertural openings provides better communication of the organism with the environment.

Some cytoplasmic structures in Foraminifera were also the consequence of the processes of polymerization in their different phyletic lines (Fig. 5.4, group D, nos. 1–6). In the more primitive unilocular agglutinated and tectinous shells of the subclasses *Astrorhizana* and *Lagynana* (class *Astrorhizata*), the cell may have one or several (polymerized) nuclei (Fig. 5.4, group D, nos. 1, 2). In the representatives of



the classes Spirillinata, Miliolata, and Rotaliata having multichambered calcareous shells the nuclei are always polymerized (Fig. 5.4, group D, nos. 3–5). The nuclear apparatus of Nodosariata has not been investigated yet. Polyploidization studied in Foraminifera only in nuclei of some representatives of the class Rotaliata (Zech 1964; Voronova and Mikhalevich 1985) represents an example of the polymerization of genomes. This is also the case in the nuclei of some other protistan groups (e.g., Radiolaria) whose genomes are also polymerized.

5.3 Processes of Differentiation in Foraminiferal Development

The process of differentiation becomes possible when there are already preformed structures consisting of numerous elemental units (Fig. 5.4, group A). The elemental units of the foraminiferal shell are represented by their chambers. The

Fig. 5.4 The details of the structure of the foraminiferal shells, apertures, wall ultrastructure, and nuclear apparatus (not to scale). *A* polymerization and differentiation of the chambers of the shell: 1, 2 unilocular shells—*Astrorhiza* (1), *Lagena* (2); 3, 4 polymerized undifferentiated chambers of equal size—*Grigelis* (3), *Saccamminopsis* (4); 5–25 chambers differentiated in size—*Lunucammina* (5), *Pseudonodosaria* (6), *Gorisella* (7), *Frondicularia* (8), *Bolivina* (9), *Stainforthia* (10), *Bulimina* (11), *Cornuspira* (12; circular proloculus followed by tubular chamber), *Dolosella* (13), *Loeblichia* (14), *Discorbis* (15), *Nummulites* (16), *Elphidium* (17), *Heterostegina* (18), *Clavulina* (19), *Discospirina* (20), *Neoschwagerina* (21), *Lepidocyclus* (22), *Orbitolina* (23), *Tretomphalus* (24), *Globigerinoides* (25); 18–25 the chambers are differentiated also in form; 21–25 the chambers are differentiated also in function; 21–23 initial large embryonal chamber; 24 a big floating chamber at the lower part of the shell; 25 the last elongated brood chamber (light in color). *B* polymerization of the main apertures: *Cribrostomum* (1), *Haplophragmella* (2), *Haueirina* (3), *Borelis* (4), *Marginulina* (5), *Amphimorphina* (6), *Sporobuliminella* (7), *Neocribrella* (8), *Anticleina* (9). *C* additional apertures (as black openings): *Trocholinopsis* (1), *Polystomammina* (2), *Norvanganina* (3), *Toretammina* (4), *Virgulinella* (5), *Cribrorhynchium* (6), *Almaena* (7), *Globigerinoides* (8); 1 Spirillinata; 2–8 Rotaliata; (1, 4, 5, 6, 8 sutural apertures; 2 umbilical apertures; 3, 7 peripheral apertures). *D* polymerization and differentiation of the nuclei: *Iridia* (1), *Myxotheca* (2), *Patellina* (3), *Quinqueloculina* (4), *Cibicides* (5, 6); 1, 2 Astrorhizata; 3 Spirillinata; 4 Miliolata; 5, 6 Rotaliata; 1 single nucleus; 2, 3 polymerized nuclei of equal size; 4, 5 polymerized nuclei differentiated into the somatic macronucleus (large, black) and generative micronuclei (multiple); 6 disintegrating macronucleus passing through the foramina (black). *E* oligomerization of the previously polymerized chambers: *Ammosphaerulina* (1), *Idalina* (2,3), *Paleopatellina* (4), *Bombulina* (5), *Dimorphina* (6), *Clavulina* (7), *Neonorbina* (8), *Orbulina* (9); 1–3 Miliolata; 4 Spirillinata; 5 Nodosariata; 6–9 Rotaliata; 1, 2, 9 last chamber enveloping the previous multichambered shell; 4, 5 diminished number of chambers in the final uniserial part; 4, 8 diminished number of chambers in the last coils of the trochospirally coiled shells). *F* the ultrastructure of the calcareous shell wall: microgranular wall with the randomly situated grains of variable size occurring in the lower representatives of all the foraminiferal classes (1), porcellaneous wall with randomly oriented needle crystals characteristic for Miliolata (2), hyaline wall with crystals situated perpendicularly to the shell surface characteristic for Nodosariata (3), hyaline wall with perpendicularly organized crystals situated in two layers and separated by the additional organic layer characteristic for the Rotaliata (4). *iol* inner organic lining serving as a wall matrix, *mol* middle organic lining between two lamellae of the Rotaliata wall. (D 1–5 after Mikhalevich 2005, 6 after Mikhalevich 2000; E after Mikhalevich 2000, modified)

chambers are separated from each other by the septa. Both chambers and septa create the compartmentalization of the shell space and of the cytoplasm in these chambers. In the simplest case the polymerized chambers are similar, equal in size and form (Fig. 5.4, group A, nos. 3, 4). But the multiple structures provide further opportunities—these multiple chambers could be differentiated. The process of differentiation is the second step in the evolutionary development. Thus, in Metazoa cells are differentiated into different tissues. In Foraminifera chambers may be differentiated in size (the simplest case) (Fig. 5.4, group A, nos. 5–25) and also in form (Fig. 5.4, group A, nos. 18–25). In some advanced genera the chambers of Foraminifera are differentiated in function (Fig. 5.4, group A, nos. 21–23, embryonal chambers; no. 24, floating chamber; no. 25 brood chamber). In this latter case the process of differentiation is tightly bound with the process of specialization. This process also took place in parallel in different classes and at different geological times. Embryonic chambers were formed in the higher representatives of the classes Spirillinata (Cretaceous orbitolins), Miliolata (Paleozoic fusulinids, Cretaceous alveolinids), and Rotaliata (Paleocene nummulitids) (Fig. 5.4, group A, nos. 21–23). Differentiation of the chamber form at the different stages of ontogenetic development occurred in each of the classes possessing multichambered forms. *Heterostegina* among Rotaliata, *Discospirina* among Miliolata, and *Orbitolina* among Spirillinata (subclass Ammodiscana) could be named as the best examples of such differentiation (Fig. 5.4, group A, nos. 18, 20, 23). Such functionally specialized chambers as the floating and brood chambers are known only within the more advanced foraminiferal class Rotaliata (Fig. 5.4, group A, nos. 24, 25).

The process of differentiation is often combined with the process of oligomerization when similar multiple structures become diminished in number. Thus, in each of the four classes with multichambered foraminiferal shells in many advanced genera the number of chambers in their last whorls in the final growth stages is less than that in their earlier whorls (Fig. 5.4, group E, nos. 1–9); for example, one chamber compared with five to ten chambers in their initial whorls. This is demonstrated in the shells with final subcircular (Fig. 5.4, group E, no. 8) or annular chambers or in the shells forming the uniserial part (Fig. 5.4, group E, nos. 6, 7). In the classes Miliolata, Nodosariata, and Rotaliata the whole multichambered shell could be entirely enveloped by the last chamber (Fig. 5.4, group E, nos. 1, 3, 9), looking from the exterior like the unilocular shell. In such cases there is a return to the previous unilocular state but on the base of a new more advanced multichambered state (new level of the developmental spire). In rare cases such oligomerization of the chambers within a single foraminiferal organism happens as a result of dissolution of the inner chamber wall and fusion of several chambers into a single one. This phenomenon occurs in Foraminifera in the class Nodosariata (e.g., *Bombulina*; Fig. 5.4, group E, no. 5). The process of oligomerization also takes place in many multicellular groups, for instance, the fusion of the breast segments in Insecta and the reduction of the number of parapodia in Polycheta.

The differentiation of the apertural system of the foraminiferal shell into the main and supplementary ones was mentioned above.

The polymerized foraminiferal nuclei were the subject of subsequent morphological and functional differentiation into somatic and generative nuclei (Fig. 5.4, group D, nos. 4, 5) in the classes Miliolata and Rotaliata. The representatives of the class Spirillinata that were studied appeared to be homokariotic (Fig. 5.4, group D, no. 3). Data on the nuclear apparatus of Nodosariata are absent.

In Metazoa the vegetative and reproductive functions are shared between different organs. The processes of polymerization and differentiation at the nuclear level are also specific features of unicellular organisms. Polymerization of the nuclei is known in such protistan groups as Filosea, Testacealobosea, and Opalinata. But the polymerized nuclear apparatus underwent the next stage of evolutionary development, namely, the differentiation of the nuclei in terms of form and function into somatic and generative ones is known only in the two large and advanced protistan groups: in Infusoria and Foraminifera. This fact along with the other advanced structures of the organisms, such as, for instance, a very complex and differentiated foraminiferal calcareous skeleton or an infusorian cytoskeleton, provides a basis for regarding both groups as taxa of a high taxonomic rank—as separate phyla (Mikhalevich 1980, 1981, 2000). During foraminiferal development the degree of polymerization and differentiation of the nuclear apparatus increased from the more primitive classes (Astrorhizata, Spirillinata) to the more advanced ones (Miliolata and Rotaliata). A similar parallel complication is accompanied by the development of the skeletal structures (Fig. 5.2).

5.4 Processes of Integration in Foraminiferal Development

In polymerized and differentiated shells, especially in the supermultichambered forms, the communication of the initial chambers with the final ones and with the environment becomes hard. The equilibrium between the organism and the surroundings is broken and the organism comes to an unbalanced state (Prigozhin and Stingers 1986). In this case the rise of the new integrative system facilitating the communication between the disintegrated parts of the organism reinstates the lost equilibrium state of the organism. This third stage (integration) is represented in the foraminiferal shells by such integrative systems as foramens, tunnels, stolons, apertural integrative systems, and systems of canals (Fig. 5.5).

The simplest of all of these systems is the system of the inner foramens between the chambers which are formed when the outer main aperture turns out inside the shell after the formation of a new chamber above the previous one during the growth process (Fig. 5.5, nos. 1–6). Such foramens occur in all four classes with multichambered shells. They permit cytoplasmic flows from chamber to chamber and migration of the nuclei along the shell during the reproductive processes (Fig. 5.4, group D, no. 6). In some more advanced genera in addition to these inner foramens new secondly formed systems of passages exist. These are tunnels and stolons. Tunnels are known in Paleozoic fusulinids, which are regarded in the new system as belonging to the class Miliolata (Mikhalevich 2004, 2006, unpublished results). They

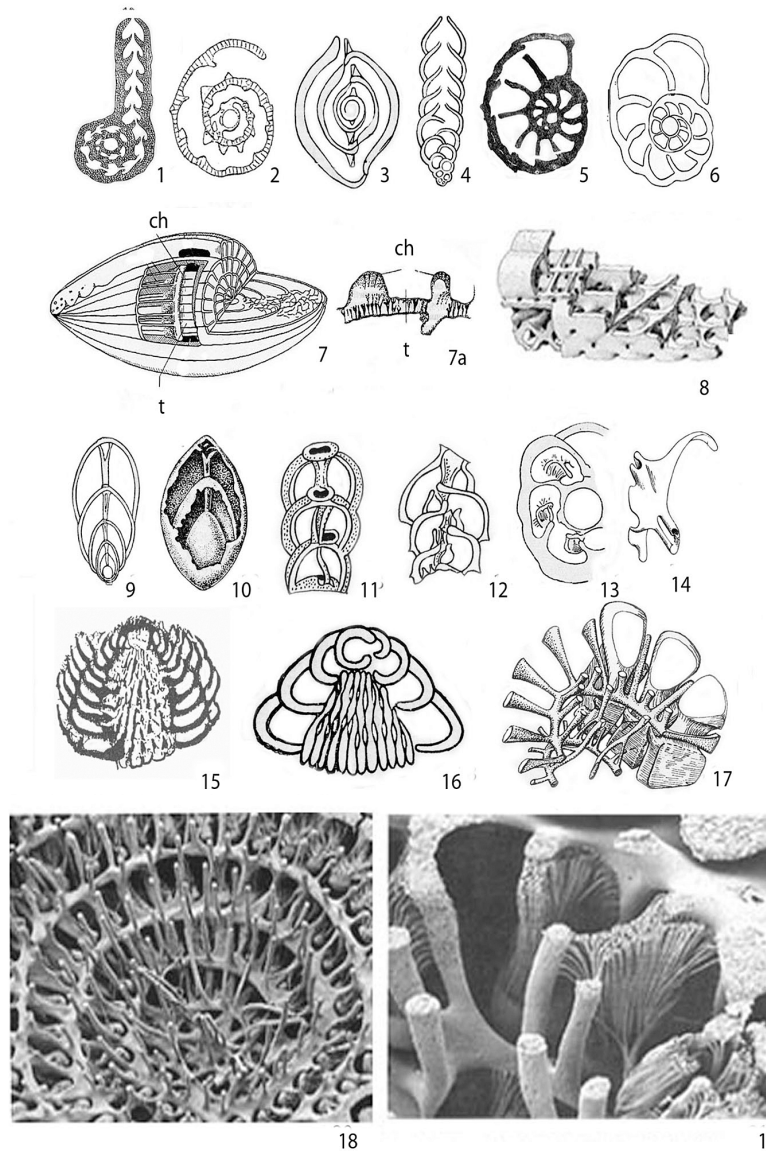


Fig. 5.5 Integrative systems in the foraminiferal shell (not to scale). 1–6 foramina between the chambers: *Ammobaculites* (1), *Melathrokerion* (2), *Pyrgo* (3), *Bigenerina* (4), *Lenticulina* (5), *Cibicides* (6). 7 chomata (*ch*) and tunnels (*t*) in Fusulinoida (7 the whole shell, 7a the detail). 8 system of stolons of *Marginopora*. 9–14 inner apertural integrative systems: *Ellipsoglandulina* (9), *Ellipsoidina* (10), *Siphogenerinoides* (11), *Eouvigerina* (12), *Reinholdella* (13 chambers with intercameral plates, 14 intercameral plate, enlarged); 9, 10 Nodosariata; 11–14 Rotaliata). 15–19 canal systems: *Lasiodiscus* (15), system of fissures in the center of the shell, *Lockhartia* (16), system of fissures between the pillars in the center of the shell, *Pseudorotalia* (17), system of tubes going between the chambers, *Elphidium* (18), *Pararotalia* (19); 18, 19 chambers are dissolved, tubes of the canals clearly seen. 15 Spirillinata; 16–19 Rotaliata. (8 after Hottinger 1978; 9–14 after Mikhalevich 2000, modified; 15 after Rauzer-Chernousova and Fursenko 1959; 16 after Sigal 1956; 17–19 after Hottinger 1979)

represent the space between the chomata—the ridgelike secondary deposits of the shell matter inside the chambers at their bottom (Fig. 5.5, no. 7a). Tunnels permit and direct in an easier way the cytoplasmic flows. The stolon system is the system of passages between the chambers, studied in detail by Hottinger (1978) (Fig. 5.5, no. 8). It is known among the representatives of the classes Miliolata and Rotaliata. Those three systems are rather primitive and do not have their own walls limiting their space.

Integrative apertural systems are developed in the classes Nodosariata and Rotaliata. They represent the inner apertural structures connected from chamber to chamber into one joined system and going inside the chamber space. In Nodosariata they are formed by the closed entosolenian tubes (*Ellipsoidina*, *Ellipsoglandulina*, *Pleurostomella*) (Fig. 5.5, nos. 9, 10). In Rotaliata they could be represented also by closed tubes (though of a character different from that in Nodosariata) or more often by half-closed tubes, grooves, tooth plates, or complexes of tooth plates of variable form (Fig. 5.5, nos. 11–14). These integrative inner apertural systems partly or fully isolate cytoplasmic flows and serve as supporting structures inside the apertures where the cytoplasmic flows are more intense. They provide full or partial differentiation of the cytoplasm inside the cell and also help to canalize the cytoplasmic streaming.

The most complex integrative system in Foraminifera is the system of canals having its own walls and going not inside but between the chambers. These systems were studied and demonstrated in the intricate works of Hottinger (1979; Fig. 5.5, nos. 17–19). Complex canal systems are developed in many higher representatives of the class Rotaliata when there are thin canal tubes between the chambers in spiral and radial directions often ramifying into the complex system of multiple thinnest tubes (Fig. 5.5, no. 19). Canal systems of the higher representatives of the class Spirillinata are less complex and differ from those of the higher Rotaliata: their tubes go between the whorls of one tubular chamber rather than between the multiple chambers of Rotaliata; their branching is not so complex or represents the system of fissures (Fig. 5.5, no. 15). In the Rotaliata themselves some more primitive “canal” systems exist, formed by the system of radial and intraseptal fissures and interocular spaces between the chambers, facilitating their communication with the environment as they are opened into the wide and partly opened umbilical area (*Ammonia*, *Lockhartia*; Fig. 5.5, no. 16). The space of these passages is separated by secondary lamellae or pillars rather than by the closed tubes of the more advanced Rotaliata representatives. The early chambers of such shells often do not even have such an integrative system of passages and are more strongly isolated. In Nodosariata a specific canal system arose only once as an exception in one genus *Delosina* (Revetz 1989) and is represented by a system of thin tubes going under the sutures and opening along them.

Hottinger (1978) showed that the ectoplasm circulates in canals supplying the cell with environmental elements, including oxygen. Thus, forming the complex ramifying system of thin and thinnest hard calcareous tubes, it plays the role of the integrative blood system in higher multicellular animals and its complexity is striking for a unicellular organism. All the last three types of foraminiferal integrative

systems (stolons, apertural integrative systems, canals) represent the systems of the new organism level in one cell, thus giving at the same time an example of the multiplication (polymerization) of the organism systems. In some genera the two types of integrative systems could be combined in one shell (for instance, the stolon system coexists with the canal system in *Nummulites* and in some other nummulitid genera). The primitive system of foramens between the chambers also always occurs in all the shells possessing the more complex integrative systems.

Each integrative system has its own material object. The material objects of tunnels are represented by chomata, stolons—by a rather complex system of alternating openings, and canals—by the system of fissures limited by the secondary lamellae in the less advanced forms and by the closed tubes in the highly advanced genera. In the case of canals their inner ectoplasmic content also represents their special material object. Similarly in the metazoan blood system the vessel's walls are composed of specialized cells and their content consists of the different types of blood cells. Of course the blood system is a much more complex plural-component and more deeply differentiated system than the foraminiferal canal system developed within one cell. But all such integrative systems permit the direction and canalization of special flows providing their special functions, thus facilitating the communication of the different parts of organisms and increasing their wholeness. They provide the interaction of the disconnected parts and the strengthening and intensification of such interaction.

5.5 Aromorphoses in Foraminiferal Evolutionary Development

With the appearance of such a complex integrative system as the canal system the foraminiferal organism achieved a new higher level of its organization, giving it new and more effective possibilities of surviving and competing with other organisms. Such significant progressive promising evolutionary changes were named by Severtzov (1925, 1939) “aromorphoses.” Later A. Panov (personal communication) called them “phase transfer,” moving the term nearer to the physical notions.

In the foraminiferal evolutionary development the rise of multichamberedness and of the complex integrative canal system are considered as such aromorphoses (Mikhalevich 1981, 2000). Among the types of secreted calcareous shell walls, microgranular and porcellaneous wall types are composed of disordered randomly oriented crystals (Fig. 5.4, group F, nos. 1, 2). In *Spirillinata*, *Nodosariata*, and *Rotaliata* their calcareous crystals are strictly oriented perpendicularly to the shell surface (Fig. 5.4, group F, nos. 3, 4). Such crystal disposition makes the shells look hyaline and often translucent. But only in the latter of these three classes are these perpendicularly organized crystals situated in two lamellae with the middle organic layer between (Fig. 5.4, group F, no. 4). In this case the wall layer is doubled in the process of polymerization. The functions of these two layers (lamellae) also differ, which can be considered as a result of the process of differentiation. The ultrastructural disposition of the calcareous crystals in the foraminiferal shell wall serves as

the material object of the shell construction. It is possible to regard the rise of the bilamellar character of the calcareous secreted shell wall of the higher Rotaliata as aromorphoses also. This type of shell ultrastructure provides a less heavy and thin wall possessing new constructive possibilities. As a result Rotaliata have three additional aromorphoses in their development compared with the class Astrorhizata and two additional aromorphoses compared with the other classes. This gave them the opportunity to develop during their geological history the most complex shell structures with the greatest degree of functional differentiation and specialization of the parts (e.g., floating and brood chambers, canals). All this in turn provided them with a new level of organization, new complexity and wholeness of the organism, higher evolutionary rates of development and new possibilities in their competition with the other groups in the environment, adaptive radiation, and expansion into new ecological niches (Fig. 5.3). Rotaliata is the only foraminiferal group which could transform from the bottom to the pelagic mode of life really getting up from the bottom.

Aromorphoses provide the organisms with the transition to a new level of organization which usually goes through the stage of a nonequilibrium, unbalanced state (Prigozhin and Stingers 1986) (see earlier). The creation of the new integrative system permits the organism to pass such an unbalanced state successfully and to preserve and enlarge its wholeness. The level of organization increases.

As described above, the processes of polymerization (with the subsequent differentiation) and integration and the aromorphoses happened in different classes of Foraminifera independently and in parallel, having in each of them similar tendencies and at the same time their own specific features.

5.6 General Character of the Main Evolutionary Regularities

5.6.1 *Different Levels of the Organization of Matter*

This chapter does not regard the other important regularities as contributors to the evolutionary process, such as block-modular principles, feedback, nonlinearity, adaptations, increase of the rate of the evolutionary change, adaptive radiation, divergence, convergence, and parallelism, symbiotic evolution, and some others, but only the main stream ways—polymerization, differentiation, integration, and the phenomenon of aromorphoses. All of them give the organism a higher degree of wholeness, activation, and mobilization of its functions owing to the increased reciprocal activity of its functional parts and their better interaction.

These rules were significantly elaborated by the Russian evolutionary school (Berg 1922, 1977; Dogiel 1929, 1954; Severtsov 1925, 1939; Schmalchgausen 1946; Beklemishev 1964; Podlipaev et al. 1974; Naumov et al. 1977; Golubowski 1994; Poljanskiy and Raikov 1977, and others) mostly for the Metazoa. Here I try to demonstrate the manifestation of these developing processes using as an example one of the groups at the unicellular level. The continuum of the evolutionary

processes of inorganic and living organic matter (biolevel) which represents the more complex level of organization and the generality of the rules of the development for both levels were shown in Krylov and Libenson (2002). They put the “mark of equation” between the biogeochemical succession and the evolution of the biosphere. Wide character of the evolutionary regularities and the possibility of their application to the lower levels of organization of matter, beginning from the physical and chemical levels, was shown in a set of publications (Larin 1977; Krylov and Libenson 2002; Libenson and Przhibelskii 2003; Krylov 2005). Social life represents the most complex higher level of the biological form of life and at the same time the highest level of cosmic life. The processes of polymerization, differentiation, and integration along with the phenomenon of aromorphoses being the general universal evolutionary rules could be applicable to human social life as well.

5.6.2 Processes of Polymerization, Differentiation, and Integration in the Development of Human Society

Let us have a brief look at the history of human society. It developed through the shoal to the genus, tribe, then from the union of tribes to the state. The number of individuals increased in the human genera and tribes (polymerization), then more significantly in the union of tribes (new level of polymerization). (This process still is continuing and mankind has now reached a population of about six billion.)

The enlargement of the society of ancient human beings and the rise of more complex social relations in the process of collective joint actions (e.g., hunting, defense against wild animals) resulted in the necessity for a communication system, of the canalization of these new relations. It was a question of survival, of integration—and language emerged, the first social integrative system of human society. For Cro-Magnon man, not being very strong physically, this was of more importance than for other human species. The rise of language gave human beings an advantage during collective actions, quicker adaptation, and regulation. It provided the interaction of the disconnected parts and the strengthening and intensification of such interaction. Even in the early human stages of development from the shoal to the genus and tribe some elements of differentiation could be marked, the most primitive of them was the division into age groups and division of labor into man's and woman's work. The further differentiation of labor in the tribe and unions of tribes caused the appearance of the three social groups: laborers, warriors, and priests. There were heralds to transfer the messages from tribe to tribe as the separate tribes needed communication between them just as the primitive multichambered foraminifera needed their foramens for communication between their chambers. The functions of such groups in ancient society differed. They were accordingly the creation of material products, security, and preservation of knowledge and information. Heralds provided communication between the tribes (prototype of the future postal service). With the advent of priests the division into physical and mental work occurred—the most important event in the evolution of human social life (Achnazarov 2002). Complex tasks in the process of joint works such as growing crops or building dams to create and enlarge

the economic surplus (the necessary circumstance permitting a society to keep and feed priests and warriors) demanded more complex structures and relations in the society for it to survive.

When the amorphous tribal society became differentiated into different social groups a new integrative system emerged—there was a state and relations governed by a system of law and legal regulations. This is an example of centralized structures overcoming dissociation. The origin of the state could be considered at the same time as an event of amorphous character. If, in the union of tribes, the chieftain was the supreme power (with the variants—sometimes he was simultaneously the leader of the bodyguard) while the other functions of management (collection of taxes, realization of justice, and many others) were not differentiated and were performed by the council of elders in the state during the processes of centralization (i.e., integration), the main part of the latter functions passed to the king, and the counts and barons preserved only the right of possession of their land. The functions of management became differentiated: special positions (and later special institutions) appeared for their execution.

The following is also one of the evolutionary rules: the limitation of the functions of the subordinate structures in favor of a higher integrative structure (the subordination of the separate foraminiferal chambers to their unicellular organism as a whole, and of the metazoan cells to the centralized multicellular organism).

Though the comparison of the state with the human organism was mentioned earlier, it had a more artistic image and likening based on domestic notions rather than on an analytical approach based on scientific knowledge. Further it did not bring to light the mechanism of development of such a similarity. In such a likening the specific differences and complexity of each of these systems existing at the different levels of their organization were not considered.

State and law systems developed from the more primitive archaic eastern monarchy and medieval monarchy to the early bourgeois society of the new time and then to the industrial and postindustrial societies of the newest time and lastly to the information society.

In the medieval state the differentiation of the previously existing social groups was continued, mainly in relation to the different kinds of human activity (e.g., multiple guilds, corporations, etc.)—"the blooming complexity" (a term used by the well-known Russian philosopher, Leontiev 1996) of the Middle Ages. The partitions between these differentiated groups were strict: belonging to a definite group was defined by origin and usually could not be changed (as an exclusion only).

With the rise of bourgeois society centralization and integration increased. Gradually the medieval fragmentation and disunity was overcome; strict partitions between the different social groups were broken. Belonging to different social groups was not defined anymore by origin, but was mostly a result of personal possibilities and achievements, and differentiation of society was carried out on account of the more specific distinctions (educational, on the basis of property, etc.). The next very important stage of differentiation of the higher integrative functions of the state was the transition of the functions of the king's personal particular order to sectoral management by means of the institutions (the beginnings of ministries), and separation of the functions of the supreme power from the functions of management.

The disappearance in the bourgeois state of the estate partitions existing before could be compared with the disappearance of the inner chamber wall (dissolution of inner septa) in some foraminifera such as in *Bombulina* (Fig. 5.4, group E, no. 5) and the secondary reestablishment of the unilocular stage of the organism at the new level of organization. In both cases the elimination of the partitions made communication of the different parts easier and created in both systems a more dynamic state. The more effective social dynamics resulted in a more developed and effective economy, thus providing to such a state advantages in international competition.

The transition from the feudal to the bourgeois state also had an aromorphic character as later did the process of transition to the recent postindustrial and information society and state. This process is not yet accomplished. This type of society consists of a big number of groups where people are differentiated and organized on the new principles mainly on the basis of their interests (not only material or industrial, but mostly wider and more variable: societies of fishermen, lovers of art, football fans, etc.). These groups are connected in the more complex and principally new systems of intercrossing and multiaspect connections resembling the human brain more with its neuron net than the blood system and forming the new “blooming complexity” at the higher level of organization.

The new process of recent integration is represented in international supratate structures (e.g., the European Union, currently including 27 countries, international currency reserves, the World Bank), in the processes of globalization. These supratate structures resemble the integrative stage of the unions of tribes but also represent a new higher and more complex level of organization.

The integrative law systems of the different types of states mentioned above developed correspondingly from the primitive feudal law to the civil law after the Magna Charta and the Napoleonic Codex.

It is possible to compare very early human society not differentiated into social groups with the primitive unilocular foraminifera not divided into chambers, and the law systems of the states of different levels of their organization with the different types of the foraminiferal integrative systems in their different taxa with the multichambered shells existing at various stages of their development and complexity. Thus, feudal law can be compared with the more primitive integrative systems of the foraminiferal shell such as tunnels and stolons (Fig. 5.5, nos. 7, 8), and the later civil law with the perfect canal system of the higher Rotaliata (Fig. 5.5, nos. 17–19). The law systems during their further development diverged into two branches which can be outlined as codified common law (based on codex—German-Romanic branch) and based on court decision (Anglo-Saxon for all four branches of law). The latter can be compared with the most advanced Rotaliata canal system; the first one with the variant of fissures (Fig. 5.5, nos. 15, 16). A society composed of different groups cannot exist without a system of law in a similar way to how the supermultichambered foraminiferal shells cannot survive without their integrative systems which provide easier cytoplasmic flows. Of course, the structures of societies with their multiple and interconnected variational components are many times more complex than the structures of one organism at the unicellular level. But the mechanisms of their development through the processes of polymerization, differentiation, and

integration and via the nonequilibrium state and new aromorphic changes to the new organizational level are the same.

The law systems are not the only integrative systems of human society. Moral and religious standards also serve as such systems as the laws do not embrace all aspects of life in human society. Each of these standards acts in its own sphere (has its special functions). Economics and business are based on legal relations. Morals represent a more ancient system (compare this with the system of simple forams in foraminifera; Fig. 5.5, nos. 1–6) which appeals to the simpler and more natural spheres of being. Religion can serve as an integrative system inside the state and as a system of the new civilization level uniting several states (Christian civilization).

5.6.3 Processes of Polymerization, Differentiation, and Aromorphoses in the Development of the Material Objects of Social Integrative Systems

Like the foraminiferal canal system and the Vertebrata blood system and like the brain for language each social integrative system also has its own material object. For the state this includes bureaucratic institutions, and for the legal system law institutions (Raskin 2001). Different cultural institutions serve as a base for different social groups of the postindustrial state. Communication service is the material object for several integrative systems at once. The evolutionary development of material objects (of different types of integrative systems) also passed through historical stages of polymerization, differentiation, integration, and aromorphoses. Whatever example is used all of them display the same regularities.

The first human production tool was a primitive stone cutting instrument; later a multitude of instruments were used, more complex, multipurposed, and specialized (nomenclature of the Late Stone Age counts dozens of them). The advent of metal instruments (firstly made from copper and bronze and later from iron) could be regarded as aromorphoses. The hand-manufactured production in the guilds of medieval times underwent a similar process of multiplication and differentiation until it was substituted by machine production. This new mode of production also represented an aromorphic change. Polymerization of the bearers could be exemplified by the polymerization in variable technical branches—multibarrel arms (revolvers), multiengine airplanes, etc.

One of the most important methods among these material objects for the integration at the social human level is the communication service which serves as a material object for several integrative systems. The line of its stages can be seen from the first heralds and sound signals to the regular postal service (relay-race horse mail, written mail) and from communications based on the wire principle (telegraph, telephone) to wireless ones based on wave principles (radio, mobile phones). In parallel the rise and development of printing and an increase in book and press publications took place. It was not by chance that the dissemination of Protestantism coincided with widespread book-printing. With the appearance of television and the Internet

and with the integration of all the communication services (television, Internet, fixed and mobile communication systems) into a unified whole there was a unified information system. The Internet represents a new type of communication that is difficult to distinguish from material matter and the integrative system itself. The recent units of countries would not be possible without a new unified communication service system as its material objects.

In the development of material objects the examples of aro-morphic changes also happened many times (invention of firearms, wireless communication service). The most demonstrative example would be the transition from the multicore processor to the quantum computer.

With the increasing complexity of human society, the number of integrative systems increases. While in the foraminiferal organism the maximum number exceeds only four, in the human organism it is about ten, and the number in human society increases dozens of times.

5.7 Conclusions

We have shown that foraminiferal multichamberedness and the different types of calcareously secreted walls of the integrative systems originated in different classes many times independently and in parallel, and not simultaneously (e.g., canals of *Lasiodiscids* in the class *Spirillinata* in the Paleozoic, and of *Rotaliata* much later, since the Upper Cretaceous).

The origin of the states had the same character, often with the existence of intermediate forms (between the feudal and bourgeois, or the early feudal and late feudal societies). The ancient primitive structures and the advanced ones usually coexist simultaneously (unilocular *Foraminifera* live in the Recent seas together with the *Rotaliata*, i.e., unicellular organisms coexist with multicellular ones; the feudal type of state coexists with bourgeois and industrial societies). Human tribes existing at the level of the Stone Age still exist in South America, where they are not even acquainted with making fire. And the newly formed structures also often contain the remnants of the previous one: some remnants of the feudal law in civil law, of the estate partitions in bourgeois society (the caste system in modern India and the House of Lords in the UK have been preserved, for example).

The transition from one organizational level to a new one occurs when the possibilities of the previous structures are exhausted. It happens as a result of aro-morphoses and usually goes through a nonequilibrium stage. Thus, the eukaryotic *Rotaliata* cells of higher complexity represent the highest level of organization at the unicellular level and the mainstream of evolution of life later went the way of multicellularity in a similar way as the previous *Procariota* level was followed by the eukaryotic way. When the potentialities of the feudal-level state were exhausted bourgeois societies arose. The material objects of human activities exemplify the same regularities. Stone tools were replaced by metal tools, hand manufacturing by factory production, mechanical principles of arms and aircraft construction by the

jet principle, etc.. In materials bearers of foraminiferal integrative systems chomata and stolons were replaced by canals. One of the best examples is seen by the changes in Japan at the end of the nineteenth century (Maidzy revolution) when the elimination of the estate compartmentalization (of saoguns) resulted in equal rights and the advent of a new effective integrative systems of the western type (including the judiciary). These were enough to make the leap in development through several centuries at once.

The recent democratic rightful state having the most advances integrative systems with the most developed material objects of these systems represents the highest level of social organization, which gives it the most effective possibilities for surviving in competition with other state systems. The foraminiferal higher class Rotaliata was not only widely distributed in at the ocean bottom but owing to its highly developed integrative systems and to such a progressive material object of its shell as the bilamellar calcareously secreted wall it was able to gain a new ecological niche and to expand into pelagic waters. Similarly the information society of the new type possesses social systems with a high level of integration and also highly organized material objects. All this gives mankind possibilities to expand into the cosmos.

This short historical discourse was made to search for the mechanisms of evolutionary changes at different levels of structural organization of organic and social life and to show the continuum of these life levels and the general character of the main evolutionary regularities (polymerization, differentiation, integration, and aromorphic changes) through time. The same mechanisms could be applied and searched for within different organizational levels of varying complexity. There was no opportunity here to go into more detailed analysis of the peculiarities of the processes of polymerization and differentiation themselves such as polymerization through the subdivision of homologous units or through their new formation and addition, and cases of differentiation after oligomerization (through the process of fusion or elimination of subunits, etc.) and only the main processes could be considered. Knowledge of all of these regularities permits not only an understanding of the evolutionary processes of the past and present but also the ability to predict ways of development for the future.

Thus, the basic evolutionary regularities elaborated first for living organisms represent general evolutionary principles applied to all levels of organization of the matter of the universe. They promote the mechanism of transition to a new level of organization and the way of further progressive evolutionary changes through time.

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