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Methods and Applications in Micropalaeontology

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Polymerization and oligomerization in foraminiferal evolution

(Figs 1–6)

Abstract. The regularities of evolutionary development were studied so far mostly at a multicellular level in the Metazoa. The analysis of the morphologic development of some Protistan groups, mainly the Foraminifera, shows that the basic rules of evolutionary development such as Dogiel's (1929, 1954) concept on polymerization and oligomerization of the structures of the organism, leading to further differentiation and integration of these structures in their morphology and functions, can be seen in the Foraminifera as well. Concerning the usually minute dimensions of the foraminiferal cell, the processes of polymerization are more developed at this level of organization than the processes of oligomerisation. Polymerization represents at the same time the prerequisites for the subsequent processes of oligomerization and differentiation.

In the foraminifera the main polymerized structures are the number of nuclei and the genomes inside the nuclei (polyploidy), the number of chambers, the number of apertural openings and elements of the inner apertural structures. The polymerized elements of the foraminiferal skeleton are subject to the process of oligomerization as well. As a consequence of the preceding polymerization and oligomerization, new organismic differentiated and integrative structures emerge: the embryonal specialized chambers, integrative structures of stolons, tunnels and channels, and integrative apertural systems. These represent a new level of polymerization, the multiplication of the organism systems. Thus these processes promote the transition to a new level of organization, open pathways to further evolutionary change, which gives the organism a higher degree of wholeness and a higher level of activity of its functions. The processes of polymerization and oligomerization are the major pathways of macroevolution. These take place in different foraminiferal groups independently and in parallel, their investigation helps to construct a natural taxonomic system.

Key words: polymerization, oligomerization, macroevolution, nuclei, skeletal structures.

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INTRODUCTION

Phylogenetic change among organisms is mostly seen in their morphological organization. As far back as 1859, Darwin had stressed the necessity of the study of the morphological regularities of the evolutionary process. What are those general principles according to which phylogenetic change of the organs, the organelles, and the whole organisms occur, which give those organisms their high degree of complexity and plasticity of their organization?

These studies were founded by Cuvier (1801) and later developed by a set of evolutionists. Especially wide investigations of morphological regularities in the evolutionary process were done by Severtzov (1925, 1939) and by his followers Schmalchgausen (1939, 1946) and Dogiel (1929, 1954). Severtzov elaborated the basic principles of comparative morphology, of morphological and biological progress, of phylembryogenesis. The progressive biological development that led to the general increase of the animal organization and the activation of vital functions, and to the opening of the way to widen ecological niches was called by him the "morphophysiological process" or "aromorphosis". Dogiel demonstrated the wide occurrence of aromorphosis.among the Protista. Dogiel was also the creator of the concept of polymerization and oligomerization. Both represent important morphological rules of the evolutionary process. He understood polymerization as the formation and presence in the organism of a great number of homologous organs in the Metazoa or organelles in Protozoa. Oligomerization was understood as the diminution of the number of homologous structures. Oligomerization is possible only when polymerization has taken place before. Both processes are connected to the differentiation of the organism in the process of evolution and are usually interconnected. Later the polymerization and oligomerization theory was developed in the studies of Podlipaev *et al.* (1974) and Naumov *et al.* (1977). These authors warned of the confusion of these processes and their results seen in the polymerous or oligomerous structures and made the notion itself more precise. The process of polymerization was defined as the process of increase in the number of homologous formations connected with the intensification of the functions of the system of these formations. The process of oligomerization – as the process of the decrease of the number of the homologous and homodynamic formations up to some definite number connected with the intensification of the functions of the system of these formations. The increased number of elements gives the summarized effect of their work.

Revising Dogiel's ideas, they established three modes of polymerization contrary to the previous four offered by Dogiel. The fourth one – the reduction – they excluded from this phenomenon. These three ideas according to Podlipaev *et al.* (1974) are: (1) Fission – the enlarging of the number of organs or organoids as a result of the division of a structure that existed previously; (2) Additional polymerization – the increase of the number of new organs or organoids by the gradual addition of new units similar to the pre-existing ones; (3) Similation – contrary to the two previous modes, in this case in the process are involved organs and organoids having a common origin, but differing in their functions when the heteromorphous structures take on similar functions (e.g., in *Bradypus* and some other animals part of the breast vertebrae take on the function of the neck vertebrae).

Multiple examples of polymerization of the organs in Metazoa are widely known (firstly the metameric organization in the high Annelid worms and in the Arthropoda, their multiple limbs and multiple repetitive branchial outgrowths, nervous, excretory and blood systems, and even more often the multiple gonads, disintegration of the cutaneous-muscular envelope of the lower worms into separate muscles in the higher ones, the faceted organization of the compound eyes of insects and many others). Also examples of oligomerization (the fusion of the metameric parts of the body and the metameric systems of organs – for example of the head and breast segments in the Insecta, of all the body segments in the Acarina) have been extensively discussed. But among the Protista these phenomena were not studied in detail, only among the most advanced protistan groups such as the Infusoria were significant observations made (Poljanskij & Raikov, 1977).

Polymerization and oligomerization – both represent two sides of a more general rule – the intensification of the functions and of the stability of the whole organism system.

I would like to emphasize here that the processes of polymerization/oligomerization discussed in the present article are restricted to one of the biological levels – the level of the organism system, and mostly of the unicellular organisms, which were less studied from this point of view. Symbiosis so profoundly studied in the classic works on this subject (Hallock, 1981a, b, 1982; Hottinger, 1982; Kuile & Erez, 1987; Lee & Hallock, 1987; Lee, 1990 and others) is beyond the limits of this study. It can be considered however as a special case of polymerization of the systems in the organism, leading to enhanced complexity of the organism and efficiency of its functions. Symbiosis is not the result of the multiplication of homologous structures (resulting of division that is not completed) but is a result of the joining of quite different structures, not homologous, of the different organisms. Thus this phenomenon represents a more complex biologic system. When symbiosis is facultative – the symbionts do not constitute a single organism with their host.

In the western scientific literature the term polymerization is used to describe only the chemical processes of the formation of polymeric compounds. Dogiel (1954) had indicated the wider character of the processes of polymerization and oligomerization. Actually, these concepts have an extremely general character that oversteps the limits of chemistry or biology, and are essentially systemic notions. The basic regularities of a general system theory permit to apply them to all structural levels of the organism. Similarities and distinctions of the processes of polymerization/oligomerization taking place at the molecular (chemical) level and biologic organismic level were discussed earlier (Naumov *et al.*, 1977; Zamorsky, 1977; Larin, 1977; Mikhelson, 1977) and are not touched upon here.

METHODS AND MATERIALS

The method of this study is the method of comparative morphology and the analysis and application of the main evolutionary regularities (polymerization and oligomerization), studied previously nearly exclusively on the Metazoa, to organisms of the unicellular level of organization, i.e., the Protista (chiefly the Foraminifera).

All the main groups of foraminifera, of wide geological range, were used for this study. To compare the developing process of the phenomena of polymerization and oligomerization in the different systematic groups and different phylogenetic lineages, the classification offered by Mikhalevich in a series of studies and in the latest one of 2004 was used. This classification conceives the phylum Foraminifera as consisting of five classes: Astrorhizata Saidova, 1980, Spirillinata Maslakova, 1990, Miliolata Saidova, 1981, Nodosariata Mikhalevich, 1992, Rotaliata Mikhalevich, 1980. The four last classes include in their composition besides the higher subclasses with calcareous shell walls (Spirillinana, Miliolana, Nodosariana, and Rotaliana) also lower subclasses with an agglutinated wall: Ammodiscana Mikhalevich, 1980, Miliamminana Mikhalevich, 1980, Hormosinana Mikhalevich, 1992, and Textulariana Mikhalevich, 1980, respectively. The class Astrorhizata includes the subclasses Astrorhizana Saidova, 1980 with an agglutinated wall and the subclass Lagynana Mikhalevich, 1980 whose representatives have a tectinous wall. The class Rotaliata includes also one more subclass of calcareous planktonic forms – the Globigerinana Mikhalevich, 1980. The understanding of the composition of the subclasses with the agglutinated representatives differ significantly from the ideas of Loeblich & Tappan (1987). The former Textulariana are therefore significantly revised (Mikhalevich, 2004).

RESULTS

Polymerization and oligomerization in the different Protistan groups

As was earlier shown by Dogiel (1929, 1954), the main evolutionary regularities can also be observed among different Protista. Thus the flagella could be polymerized in the Mastigophora from one or two to 4 and 8 and could become multiple in the Hypermastigida (Fig. 1: *1–11*). The enlarging of the number of flagella gives the animal the possibility of quicker and more complex movements. In *Trichomonas* differentiation of the flagella takes place and in one of them is transformed into the undulate membrane, thus permitting more variable actions (Fig. 1: *8*). The multiple infusorian cilia giving the entire ciliate covering are also considered as polymerized flagella. (Fig. 1: *12*, Fig. 2: *15*). It is also possible to consider as polymerization not only of the kinetid structures but also the chromatophores and pirenoids in the Mastigophora, the mitochondria and centrioli in many protistan groups, the enlarging of the number of skeletal crossbars and of the number of the chambers in Paleozoic Spumellaria and Nassellaria (Radiolaria), of the number of inserted rims in the Diatomea (Fig. 1: *17*) and of the number of nuclei in many protistan groups (Fig. 2,

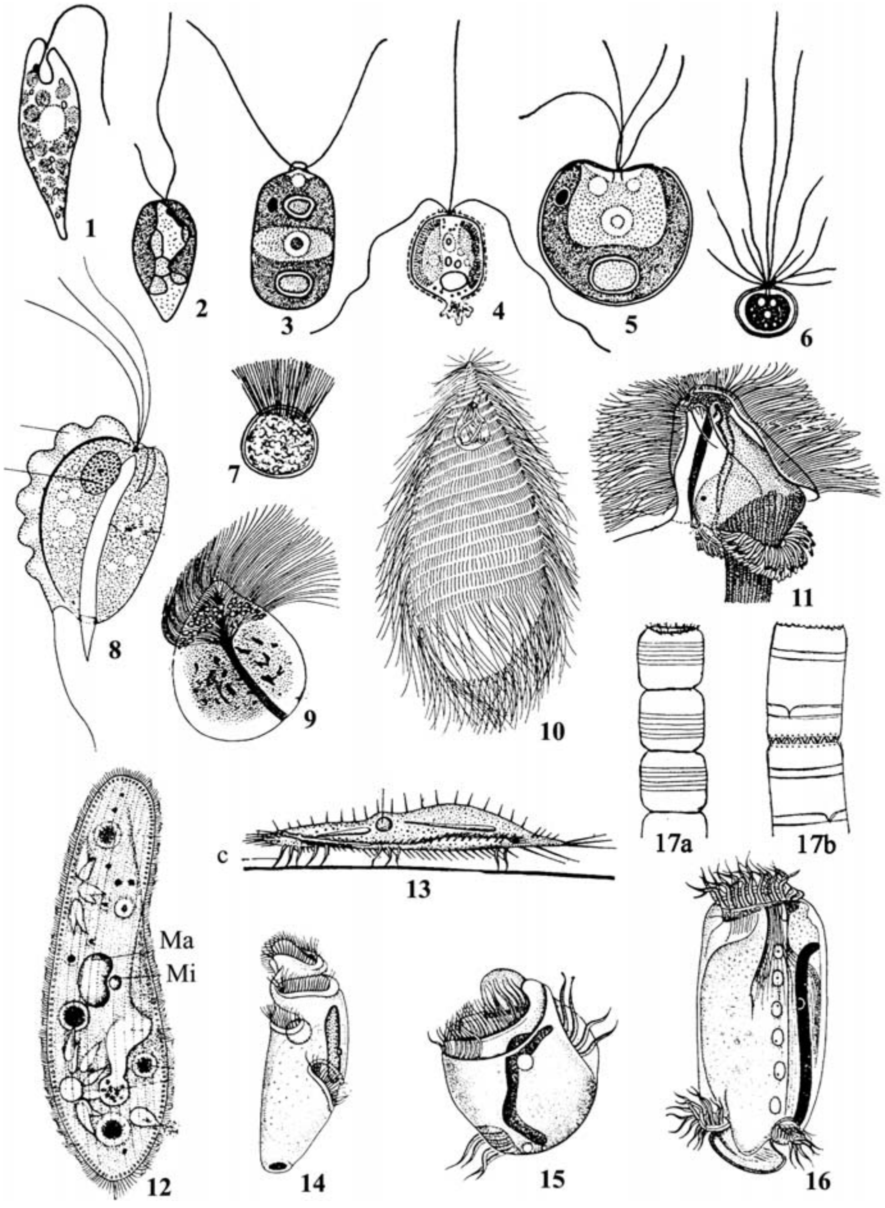
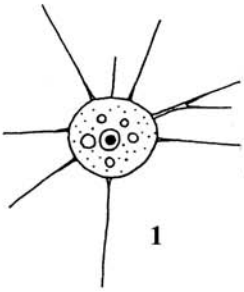


Fig. 1. The polymerized and oligomerized structures in the different protistan groups. ***1–11*** – the polymerization of flagella (*1 – Euglena proxima*, *2 – Ochromonas ludibunda*, *3 – Chlamydomonas pertusa*, *4 – Chrysochromulina kappa*, *5 – Platymonas cordiformis*, *6 – Schizochlamys galatinosa*, *7 – Derbesia neglecta* (zoospore) (1–7 – from Gollerbach, 1977), *8 – Trichomonas* sp., *9 – Calonympha grassii* (from Zenkevich, 1968), *10 – Holomastigotoides tusitala* (from Grell, 1956), *11 – Joenia annectens* (anterior part) (from Hollande & Valentin, 1969); ***12*** – polymerized cilia in Infusoria *Paramecium caudatum (*Ma – macronucleus, Mi – micronucleus) (from Zenkevich, 1968), ***13–16*** – oligomerization of cilia into cirri (from Zenkevich, 1968) (*13 – Stylonichia mytilus*, c – cirri, *14 – Spirodinium equi*, 15 – *Triadinium galea, 16 – Cycloposthium bipalmatum*); ***17*** – the polymerized inserted rims in Diatomea (a – annular rims in *Lauderia*, b – collar-like rims in *Stephanodiscus*)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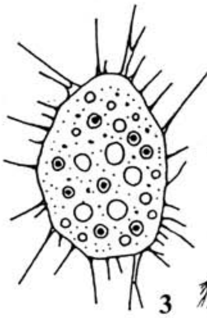
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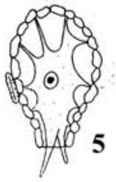
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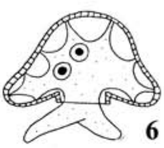
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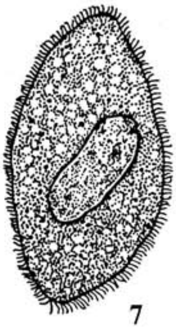
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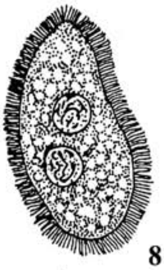
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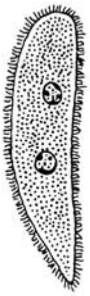
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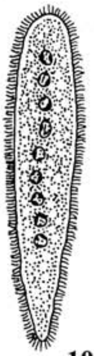
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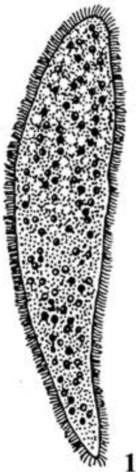
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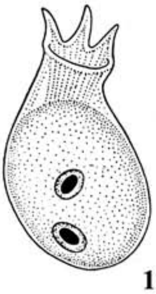
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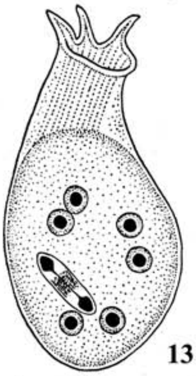
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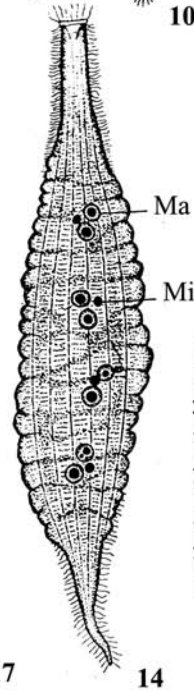

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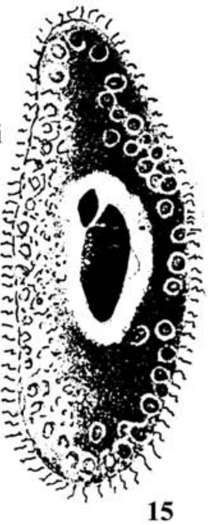
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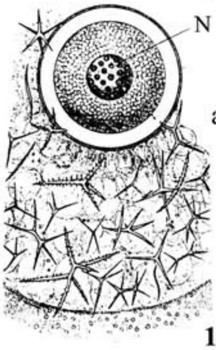

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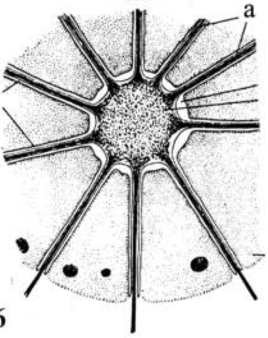

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1–15): in some Amoebae (*Nuclearia simplex, N. delicatula, Arachnula impatiens* – from 2 to 50 – Fig. 2: *1–4*), in Testacea (1 or 2) (Fig. 2: *5, 6*), in Acantharia, in Opalinata (Fig. 2: *7–11*), in Diatomea (from 1 to 8), in the lower Infusoria (*Stephanopogon, Trachelonema*) (Fig. 2: *12–14*). The very interesting phenomenon could be observed in some Radiolarians (e.g., *Sphaerellaria* – Fig. 2: *17*) when the axoplast (the system of the stiff microtubular axes of the radial pseudopodia) penetrates the very nucleus, thus forming a complex specific structure of a higher level of organization.

Polymerization of the nuclei and some cytoplasmic structures in the foraminifera

Foraminiferan nuclei are also touched by the process of polymerization. Though the nuclear apparatus was observed only in approximately two hundred species and the detailed study of the gradual changes of this apparatus during the generative cycles (at least partial) was made in half that amount, nevertheless it is possible to draw some conclusions. The majority of the representatives of the subclasses Lagynana and Astrorhizana (*Saccammina alba, Iridia lucida* – Fig. 3: *4, 5*) (class Astrorhizata) as far as it is known are mononucleate, but in some genera the polymerization of nuclei took place, for example in the subclass Lagynana in *Boderia* (from 1 to 10 nuclei), in *Ophiotuba* (many small nuclei), in *Dactylosaccus* (1 to 2 nuclei), in *Penardogromia* (1 to 20 sphaerical nuclei) (Fig. 3: *1*). In the recent Spirillinata in the agamonts of *Patellina* and *Spirillina* polymerized nuclei were also observed (Berthold, 1977) (Fig. 3: *6, 7*) as well as in the lower agglutinated representatives of the Rotaliata, subclass Textulariana – in Trochammina sp. with up to four similar nuclei in its proloculus (Pawlowski *et al.*, 1995) (Fig. 3: *10*). All these multinucleate species are homokaryotic. In the higher calcareous representatives of the classes Rotaliata (subclasses Rotaliana, Globigerinana) and Miliolata (subclass Miliolana) there is another, more advanced type of the polymerized nuclei in which the nuclear apparatus is differentiated into somatic and generative nuclei. The somatic nucleus

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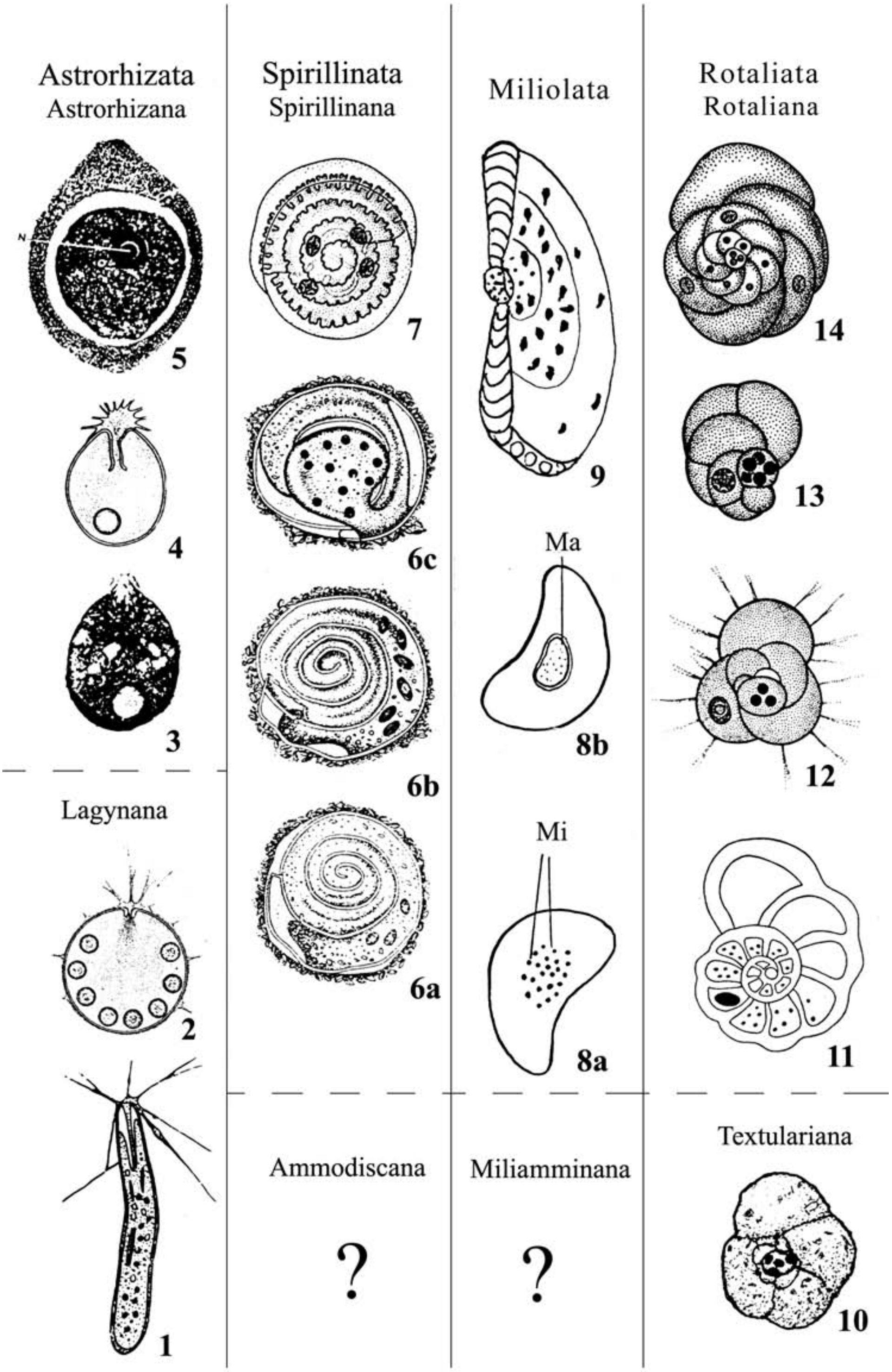
Fig. 2. The polymerization and oligomerization of the nuclei in the different protistan groups. ***1–4*** – polymerization of the nuclei in Amoebae (homokariotic), cl. Filosea (from Alimov, 2000) (*1, 2 – Nuclearia simplex*, *3 – N. delicatula*, *4 – Arachnula impatiens*); ***5, 6*** – polymerization of the nuclei in Testacealobosea (homokariotic), cl. Lobosea (from Alimov, 2000) (5 – *Difflugia* sp., 6 – *Arcella* sp.); ***7–11*** – polymerization of the nuclei in Opalinata (homokariotic) (from Alimov, 2000) (*7 – Hegneriella dobelli*, *8 – Zelleriella macronucleata*, *9 – Protoopalina intestinalis*, *10 – Protoopalina axonucleata*, *11 – Cepedea dimidiata vulgaris*); ***12–15*** – polymerization of the nuclei in Infusoria (12–14 – from Raikov, 1978, 15 – from Grell, 1956) (*12, 13 – Stephanopogon colpoda*, homocariotic, *14 – Trachelonema oligostriata*, heterokariotic, with multiple nuclei combined in groups of two Ma and one Mi, *15 – Paramecium bursaria*, heterokariotic, with oligomerized macronucleus and micronucleus); ***16, 17*** – polyploidized nuclei of Radiolaria: *16 – Lamoroxanthium pandora*, N – nucleus, *17* – axoplast inside the nucleus of *Sphaerellaria,* a – axopodii, ax – axoplast (16 – from Fursenko & Rauzer-Chernousova, 1959, 17 – from Schulman & Reshetnjak, 1980)


Astrorhizata
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Miliolata
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Ma
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Mi
8a
Miliamminana
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Rotaliata
Rotaliana
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Textulariana
10

(Macronucleus) is usually singular and large, while the generative nuclei are small and multiple, from tens to hundreds and thousands in different species. The volume of the somatic nucleus can exceed that of the generative, by two, ten, and even a thousand times. The Macronucleus also contains three times more RNA than the micronucleus, more proteins, there are also some other differences in their structure. The DNA quantity does not usually differ in both types of the foraminiferal nuclei. The separation of the functions results in the morphological differences of these differentiated nuclei. The well known examples of nuclear duality in the foraminiferal agamonts are *Cibicides lobatulus, Rotaliella heterocariotica, Metarotaliella parva* (Rotaliana*), Globigerina bulloides* (Globigerinana), *Peneroplis pertusus*, *Sorites marginalis* and *Quinqueloculina* sp. (Miliolana) (Fig. 3: *8, 9, 11–14*). In some representatives of both classes polymerization of the somatic nuclei also took place. The agamonts of *Sorites marginalis* (Miliolana), of *Rosalina columbiensis, Glabratella sulcata* (Rotaliana), possibly of *Globigerinoides ruber* (see Lee *et al.*, 1965) (Globigerinana) have not one, but several somatic nuclei (Fig. 3: *9, 14*).

Comparison of the structure of the nuclear apparatus at different stages of the life cycles in the lower agglutinated unilocular foraminifera (*Myxotheca arenilega*, *Saccammina sphaerica*, *S. alba*, *Ovammina opaca*, *Allogromia laticollaris*) (Grell, 1973; Hedley, 1962; Dahlgren, 1967) with that of the advanced calcareous Rotaliata (*Cibicides lobatulus* for instance) shows significant differences between them. The mononucleate stage in the life of the agamont of the lower agglutinated unilocular forms is more prolonged. Their young agamont is mononucleate and sometimes continues to be so in the adult stage, and only before the formation of the gamonts, after a series of mitotic divisions, it becomes multinuclear (*Myxotheca arenilega* (Fig. 3: *2*). While in the forms of higher organization only the zygote is

Fig. 3. Polymerization of the nuclei in the different classes of Foraminifera (here and further the boarders between the classes are marked with the unbroken line, between the subclasses – with the dotted line). ***1–5* – class Astrorhizata** (1, 2 – subclass Lagynana, 3–5 – subclass Astrorhizana): *1 – Penardogromia linearis*, multinucleate (from Loeblich & Tappan, 1987); *2 – Myxotheca arenilega,* multinucleate agamont)(from Grell, 1956); *3 – Psammophaga simplora*, polygenomic (polyploidized) nucleus (from Arnold, 1982), *4 – Iridia lucida,* agamont nucleus (after Fursenko & Rauzer-Chernousova, 1959), *5 – Saccammina alba*, supposedly agamont (from Headley, 1962); ***6, 7* – class Spirillinata**, subclass Spirillinana, homokariotic, *6 – Spirillina vivipara*, a, b, c – the enlarging of the number of nuclei during the agamont (shizont) stages) (from Le Calvez, 1953); *7 – Patellina corrugata*, agamont (from Zech, 1964); ***8, 9*** – **class Miliolata**, subclass Miliolana, *8 – Quinqueloculina* sp., transverse slice of the chamber cytoplasm, a – micronuclei, b – slice of the elongated macronucleus (from Mikhalevich, 1992), *9 – Sorites marginalis*, schematic section of the shell with the hundreds of micronuclei in the embryonic apparatus and the inner chambers (small) and several tens of the macronuclei (large), mostly in the intermidiate chambers, a few in the inner or outer chambers (adopted scheme after Muller-Merz & Lee, 1976); ***10–14* – class Rotaliata** (10 – subclass Textulariana, 11–14 – subclass Rotaliana), *10 – Trochammina* sp., homokariotic (scheme after Pawlowski *et al.*, 1995), *11 – Cibicides lobatulus* (from Mikhalevich, 2000), *12 – Rotaliella heterocaryotica*, *13 – Rubratella intermedia*, *14 – Glabratella sulcata*, with three macronuclei and several micronuclei (*11–14* – heterokariotic, from Grell, 1979)

mononucleate, the agamont has several nuclei beginning from its earliest stages (*Cibicides lobatulus, Metarotaliella parva, Rotaliella heterocariotica*). It is interesting to note that in the unilocular tectinous *Allogromia laticollaris* the agamont I is mononucleate, the agamont II – multinucleate (Lee & McEnery, 1976). Obviously the stage with the regenerating nuclei in the process of preparing for the cell division became fixed during the evolutionary development in the process of natural selection as the more durable stage of their life cycle.

The polymerization of nuclear material takes place in the Foraminifera as well as in some other Protistan groups, not only at the organelle level (the polymerization of the nuclei) but also at the molecular level – the polymerization of the quantity of DNA in the nucleus. In the *Cibicides lobatulus* agamonts the DNA content can increase 20–30 times (Voronova, 1979; Voronova & Mikhalevich, 1985). A similar phenomenon was reported for *Patellina corrugata* and *Rotaliella heterocariotica* (Zech, 1964), and for the primitive unicellular agglutinated species *Psammophaga simplora* (Arnold, 1982) (Fig. 3: *3*). In all these cases it is possible to speak of the polyploidization – the polymerization of the genomes. Some advanced Radiolaria also have a highly polyploid nucleus (Fig. 2: *16, 17*). In Infusoria the polyploidy of the macronucleus also takes place.

The usual pathway of the nuclear apparatus evolution is the polymerization of the nuclei, then the polymerization of the genomes (polyploidy) and the subsequent oligomerization of the nuclei. In the Foraminifera in contrast to the Infusoria the oligomerization of their nuclei is not known.

The primitive Infusoria have several polymerized nuclei (Fig. 2: *12, 13*) or polymerized macronuclei and micronuclei (*Stephanopogon*, *Trachelonema*) (Fig. 2: *14*). In the higher Infusoria only one macronucleus and one micronucleus exist as a result of oligomerization (Fig. 2: *15*). Polyploidy as well as polymerization of the nuclei also arose as the result of the division of the nucleus not completed up to the end. In the case of the polyploidy the processes are taking place inside the nucleus. Both processes of nuclear polymerization in the foraminifera take place at two different levels, resulting in the activation and immobilization of functions of the nuclei and the whole animal. It is possible to suppose that just the multinuclear and polyploid nuclear apparatus permits some representatives of this protistan group to achieve large dimensions of several centimeters and a long life span of one year or even more, which are so unusual among the unicellular organisms. The necessity of centralization and integration in such large protists having beyond that such a large and complex multichambered shell with chambers that are relatively autonomous also demands the efficiency of the functions and the complication of their nuclear apparatus.

In the foraminifera the cytoplasm itself can be involved to some extent in the process of polymerization. In the lower unilocular foraminifera it is not differentiated into endo- and ectoplasm and very weakly so in the more advanced species, usually without a definite border between its inner and outer parts. However, in the highest specialized forms of the class Rotaliata (subclass Rotaliana – Rotaliidae, Elphidiidae, Nummulitidae) as was first shown by Hottinger & Dreher (1974) and

Hottinger (1978), the ectoplasm is strongly separated and specialized in its function: in the forms having a canal system the ectoplasm is circulating in canals thus even having its own walls (Hottinger, 1978). Similar ectoplasm is obviously circulating in the canals of *Delosina* (subclass Nodosariana) – the unique representative of this group owning a canal system. A primitive canal system exists also in some pseudotwochambered higher Spirillinata (Hottinger, 1976; Mantzurova & Gorbatchik, 1982): in *Lasiotrochus* – Lasiodiscidae Reytlinger, 1956; *Hottingerella* – Hottingerellidae, Mikhalevich, 1993; *Spirotrocholina* – Spirotrocholinidae Mikhalevich, 1993. The ectoplasm circulating in canals plays a physiological role comparable to some extent with that of the blood system of the higher animals. In the other Rotaliata subclass – in the Globigerinana the outer ectoplasmic layer is very wide, forming in *Hastigerina* the bubble capsule resembling the radiolarian kalymma. This wide ectoplasmic layer plays a role in flotation. The separation of the cytoplasm into two layers also represents polymerization and with the further differentiation of their functions it results in the activation of their special activity.

Polymerization of chambers in the foraminifera

Another Foraminiferal structure undergoing the process of polymerization concerns the hardparts or test – their skeleton. The foraminiferal shells are unilocular or multichambered. The process of forming the multichambered shell belongs to the process of polymerization. Among the three main modes of polymerization defined by Podlipaev *et al.* (1974) Foraminifera use two of them: fission and additional polymerization. As an example of the first one it is possible to indicate the partial subdivision or full division of the chamber lumen by constrictions of the wall (Fig. 4: *1, 5, 14, 15, 25, 26, 29*), by the invasion of the outer wall inside the chamber (Fig. 4: *7, 10, 37*), by the formation of the septa or hemisepta dividing or subdividing the chamber lumen (Fig. 4: *2, 3, 6, 17, 21, 23, 24, 35, 44–46*), by the inner deposition of skeletal matter (Fig. 4*: 13, 22*). These ways of separating the chamber lumen arose independently and in parallel in the different foraminiferal classes and subclasses with the more primitive tectinous or agglutinated walls as well as in subclasses with the different types of calcareous walls. It may result in the formation of new chambers (which we call pseudochambers (Fig. 4: *5, 8, 14, 15, 25, 26, 29*) in contrary to true chambers formed under additional polymerization) or only the new parts of the chambers formed as chamberlets or simply representing part of the more or less isolated chamber space (Fig. 4: *10, 21, 23, 24, 44–46*). The fission mode of polymerization dominates as the basic mode in the more primitive groups (Fig. 4): in the class Astrorhizata, in the lower representatives of the subclasses Spirillinana, Miliolana, Nodosariana (not in Rotaliana). In the higher representatives of the subclasses Miliolana and Rotaliana (Fig. 4: *16–24, 36–4*5), more rarely in Spirillinana (Fig. 4: *10*), only in one or two cases in Nodosariana (Fig. 4: *35*) it occurs along with additional polymerization as the second supplemental mode of polymerization when true chambers are divided into chamberlets. In this case it is possible to speak of a mixed or multiphase ("multistored" in terms of Russian scientists) polymeriza-

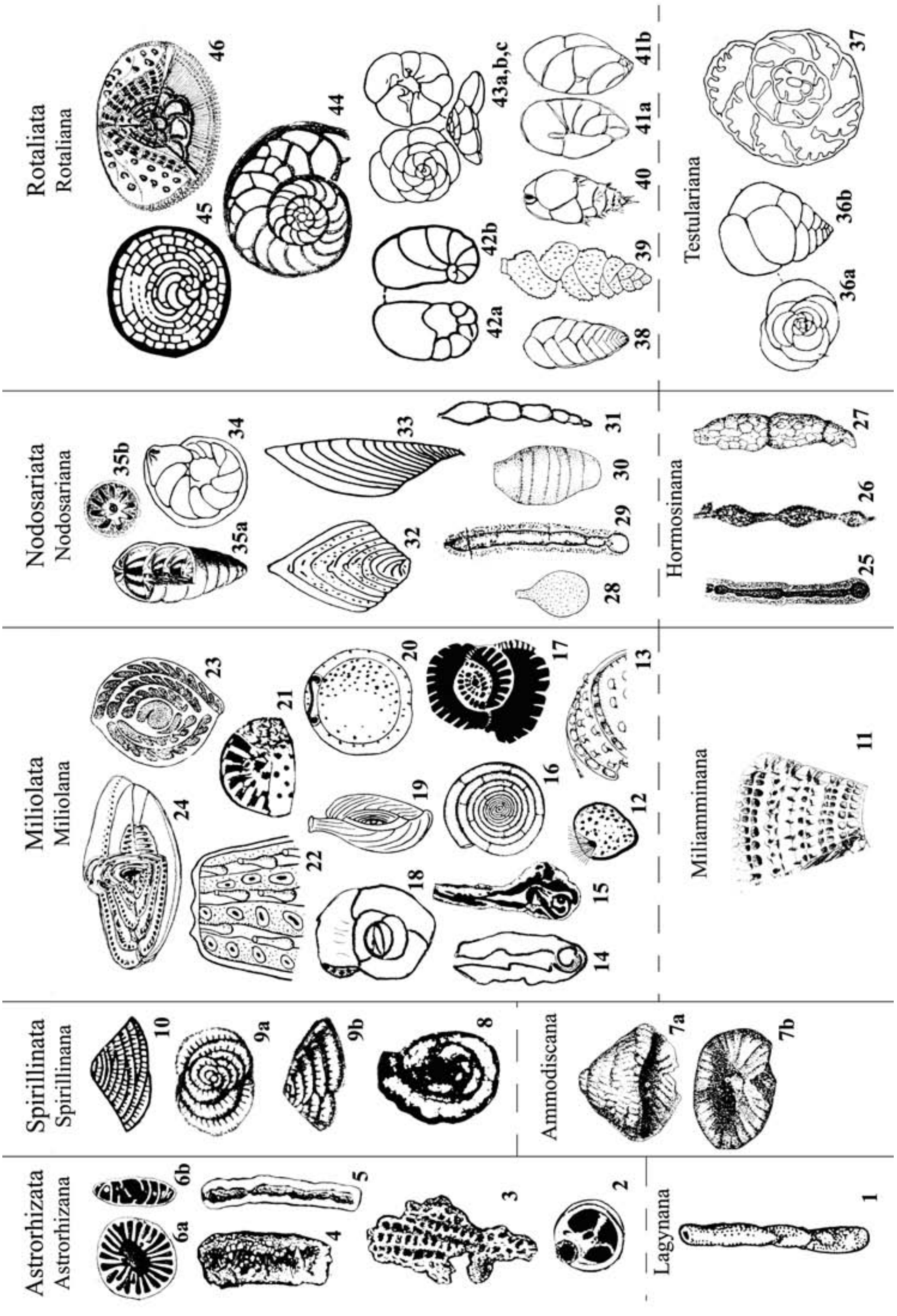
Astrorhizata
Astrorhizana
6a
6b
4
5
3
2
Lagynana
1
Spirillinata
Spirillinana
10
9a
9b
8
Ammodiscana
7a
7b
Miliolata
Miliolana
24
23
22
21
20
19
18
17
16
15
14
13
12
Miliamminana
11
Nodosariata
Nodosariana
35a
35b
34
33
32
31
30
29
28
Hormosinana
25
26
27
Rotaliata
Rotaliana
45
46
44
42a
42b
43a,b,c
38
39
40
41a
41b
Testulariana
36a
36b
37

Fig. 4. **Polymerization of the chambers in the different classes of Foraminifera.** ***1–6* – class Astrorhizata** (1 – subclass Lagynana, 2 – 6 – subclass Astrorhizana), inner divisions and subdivisions of the unilocular shells (fission): *1 – Xenothekella* with growth constrictions, *2 – Pseudowebbinella* subdivided by short radial partitions, *3 – Kerionammina*, irregular partitions forms subquadrate chamberlets, *4 – Botellina* subdivided by the protrusion of the sponge spicules of the wall, *5 – Protobotellina* subdivided by the protrusion of the sponge spicules of the wall and wall constrictions *6a, b – Daitrona* nearly completely subdivided by radial semisepta; ***7–10* – class Spirillinata** (7 – subclass Ammodiscana, 8–10 – subclass Spirillinana): *7 – Valvulinella*, chambers subdivided into chamberlets, *8 – Tournarchaediscus* with intercameral partial subdivisions by the constrictions of the wall in the last whorl of tubular chamber, *9a, b – Pseudopatellina*, multichambered, *10 – Patellina*, proloculus followed by the tubular chamber, then multichambered with short radial septula of the first and second order; ***11–24* – class Miliolata** (*11* – subclass Miliamminana, *12–24* – subclass Miliolana), new chambers formed under additional mode of polymerization and by the subdivision of the chambers as a result of fission, beginning from unilocular shell: *11 – Broeckinella* (Biokovinoidea), scheme showing the complex system of inner vertical and transverse partitions, in the marginal zone of the shell with short secondary partitions, resulting in a polygonal meshwork (after Hottinger, 1967), *12 – Squamulina*, unilocular, *13 – Shanita*, with the inner pillars, *14 – Sarmatiella*, with pseudochambers, *15 – Orthella*, with pseudochambers, *16 – Dolosella*, *17 – Pseudohauerina*, chambers subdivided by short radial septula, chambers in one whorl nearly equal, *18 – Hauerina*, *19 – Sigmoilina*, *20 – Pyrgo*, *21 – Rhapydionina*, with vertical radial septula subdividing the chambers, *22* – inner pillars in the *Archaias* chamber, *23 – Riveroina*, chambers subdived by the oblique radial septula, *24 – Alveolina*, supermultichambered shell, with tunnels, numerous septula perpendicular to the septum form chamberlets; **25–35 – class Nodosariata**, (25–27 – subclass Hormosinana, 28–35 – subclass Nodosariana), new chambers formed mostly by the additional mode of polymerization and by the fission, beginning from unilocular shell: *25 – Hyperammina*, with pseudochambers, *26 – Hormosinella*, with pseudochambers, *27 – Reophax*, with true chambers, *28 – Lagena*, unilocular, *29 – Syzrania*, with pseudochambers, *30 – Lingulina*, megalosphaeric form, *31 – Nodosaria*, *32 – Flabellina*, *33 – Citharina*, *34 – Robulus*, (30–34 – with true chambers), *35 – Multiseptida*, multichambered, with vertical radial partitions of the chambers; ***36–46* – class Rotaliata** (36, 37 – subclass Textulariana, 38 – 46 – subclass Rotaliana), exclusively multichambered, the mode of fission present as an additional way of chamber subdivision): *36a, b – Eggerella*, *37 – Remaneica*, with the secondary septula formed by the invagination of the outer wall, *38 – Bolivina*, *39 – Eouvigerina*, *40 – Bulimina*, *41a, b – Robertina*, 42a,b – *Cancris*, *43a, b, c – Discorbis*, *44 – Heterostegina*, supermultichambered, with chamberlets formed by complete secondary septa in the elder volutions, *45 – Crespinina*, microsphaeric form with finally annular chambers, divided by the radial partitions formed by infolding of the outer wall, *46 – Sulcorbitoides*, supermultichambered, with pillars and radial plates (scheme after Frost, 1974) (*44–46* – supermultichambered)

tion. The comparative morphological differences of the formation of the inner chamber compartments in some definite groups having a different character of shell wall were analyzed by Hottinger (1978, 2000). Here, only the parallel evolutionary development of the fission mode of polymerization in the different foraminiferal groups is generalized.

Under the second mode of polymerization (additional polymerization) the chambers can be of equal or nearly equal size (which occurs more rarely, e.g., *Dolosella* – Fig. 4: *16*) or differ significantly in dimensions, usually rapidly increasing in size in the process of growth (in the majority of cases, Fig. 4: *18–20, 23, 24, 31–35, 36–45*). The first case could be considered to be more primitive, as in the second case the size differentiation is taking place on the basis of the preceding polymerization. The majority of species of the classes Miliolata and Nodosariata as well as all representatives of the class Rotaliata used this second mode in their evolution. In some higher Spirillinata, this mode of the formation of new chambers also exists [in *Patellina* – Fig. 4: *10*, in *Patellinella, Paleopatellina* and *Coleiconus* (supposingly belonging to the lower Spirillinata, see Mikhalevich, 2004, further investigations are necessary) – Fig. 5: *1–3*)] though their two-chambered forms with the long tubular second chamber are referred to as pseudochambered tests because their proloculus is separated from the second chamber only by a slight constriction of the wall.

In two groups – in the higher Miliolata (order Alveolinina) and the higher Rotaliata (orders Rotaliida, Nummulitida) – the polymerization of the chamber number may result in an extremely large number of chambers, achieving hundreds and thousands of them as compared to the usual numbers of several tens. These super-multichambered, large shells (e.g., Fig. 4: *24, 44, 46*) need to organize themselves in a new way during their evolution to avoid many problems connected to large dimensions and to the difficulty of communication of their different parts with each other and with the environment. The surface area to volume ratio in the organism changes with the increase of its dimensions and the power of the functions related to its surface (such as sensitivity, respiration and so on) is diminished in this case. To withstand environmental competition the organism needs to undergo a morphological reconstruction. New systems integrating the multiple chambers arose – systems of tunnels (in the Fusulinoida) and canals in Rotaliata. The canal systems of Spirillinata did not arise on the basis of supermultiple chambers as in the two previous cases but as a consequence of the increase in the number of volutions of the tubular chamber. The stolons in Rotaliata and Miliolata and the preseptal passages of the higher Miliolata (Alveolinids) can also be considered as integrative systems. In all these cases the newly arisen systems represent systems on a new organism level. Their fine structure and disposition were shown in detail by Hottinger (1978), Billman *et al.* (1980) and others. Thus the polymerization of a number of organism systems takes place based on the polymerization of structures of a lower level. For this reason the higher Miliolata and Rotaliata as well as to some extent the higher Spirillinata could be considered as the more complex and advanced groups among the foraminifera.

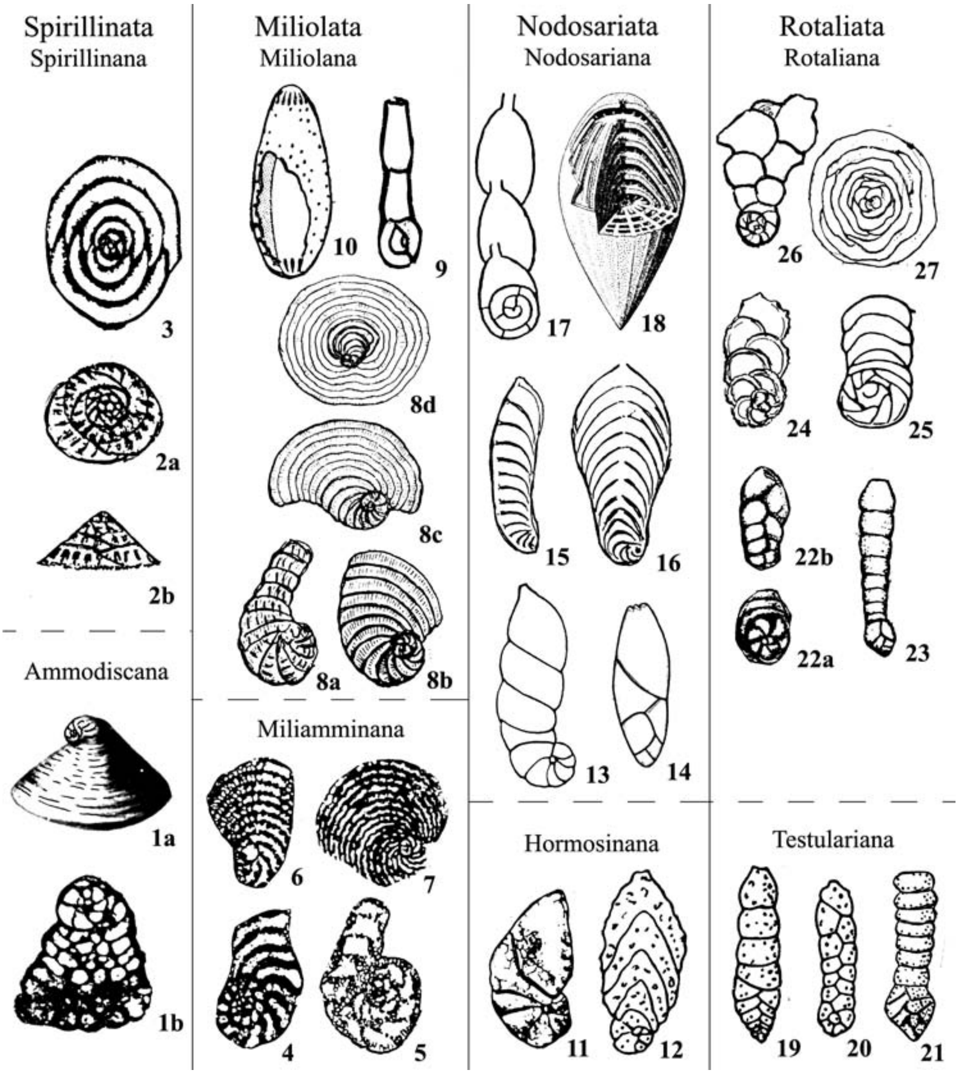

Fig. 5. Oligomerizations of the chambers in different foraminiferal classes. ***1–3* – class Spirillinata** (1 – subclass Ammodiscana, 2, 3 – subclass Spirillinana): 1a, b – *Coleiconus*, b – section, 2a,b – *Patellinella*, 3 – *Paleopatellina*, five chambers in the initial whorl, two chambers in the last whorls; ***4–10* – class Miliolata** (4–7 – subclass Miliamminana, 8–10 – subclass Miliolana): 4 – *Feurtillia*, 5 – *Pseudocyclammina*, 6 – *Alzonella*, 7 – *Flabellocyclolina*, 8a–d – different species of *Peneroplis*, 9 – *Articularia*, 10 – *Idalina*; ***11–18* – class Nodosariata** (*11, 12* – subclass Hormosinana, *13–18* – subclass Nodosariana): *11 – Ammomarginulina*, *12 – Flabellammina*, *13 – Vaginulinopsis*, *14 – Pyrulina*, *15 – Astacolus*, *16 – Palmula*, *17 – Dimorphina*, *18 – Colaniella*; ***19–27* – class Rotaliata** (*19–21* – subclass Textulariana, *22–27* – subclass Rotaliana): *19 – Bigenerina*, *20 – Bolivinopsis*, *21 – Clavulina*, *22a, b – Caucasina*, a – view of the initial trochospiral part, side view with the biserial last chambers, *23 – Rectobolivina*, *24 – Siphonides*, *25 – Rectoeponides*, *26 – Dyocibicides*, *27 – Cyclocibicides*

Another example of the increasing of the number of the structural levels in the supermultichambered forms is the differentiation of these polymerized chambers in their structure and function within one organism, thus resulting in the polymerization of different layers of chambers. The multiple examples of such differentiated chambers with usually more complex inner structure in the later whorls can be found among the lower and higher Miliolata [in Schlumbergerinana – in Biokovinoidea (e.g., Pseudochoffatellinae), Vaniinoidea, in the Loftusiida, in Miliolana – in *Periloculina*, in Rhapydionidae, Alveolinidae, Soritidae], in the higher Rotaliata (in Heterosteginidae, Nummulitidae and in some others), in the Ataxophragmiida (group of unclear taxonomic position, see Mikhalevich, 2004) in the Orbitolinidae (where the layers of chambers with different inner structure are strikingly demonstrative – Mikhalevich, 2000), Coskinolinidae, the less examples among Spirillinana (Patellinidae, Chapmaninidae). Special embryonic chambers forming an embryonic apparatus in some of the above mentioned groups also represent a striking example of such specialized additional structure of chambers (Mikhalevich, 2000, pl. 532).

Polymerization can be simultaneous, when homologous structures are formed at the same time (moment of growth) [the primary multiple apertures of *Astrorhiza, Guandiella* and others – Fig. 6: *1–4*; the secondary multiple aperture on the apertural face – Fig. 6: *25–28* (see below); some septula inside the chamber]. It also can be successive, such as the repetitive addition of the new chambers in the multichambered foraminiferal shells during their growth, extended in time.

The polymerization of chambers in the foraminiferal shell also results in the intensification of the functions and in the rising of the energy of the whole organism. The subdivision of a large chamber lumen into smaller compartments plays the same metabolic role (Hottinger, 2000).

A special case of primitive additional polymerization is represented by the pseudocolonial forms existing among the Astrorhizata (e.g., *Sorosphaera*, *Ammopemphix, Webbinelloides*) when the polymerized unilocular shells live together, but the chambers are not organized in regular order and the connections between these chambers are weak. The whole group in this case does not create an organism of higher level such as do the true colonial forms. The biology of the foraminiferal pseudocolonial species is studied insufficiently.

Oligomerization of chambers in the foraminifera

In the polymerized structures processes of oligomerization often take place. This phenomenon in the multichambered shells is usually expressed in the decreasing number of chambers in the last whorls compared with the initial ones (Fig. 5). Thus in planispiral and trochospiral shells with several chambers per whorl in their initial part, these may be only 3 or more often 2 opposite chambers in the last volutions, or the last chambers turn into circular and annular ones. In monoaxial forms with planispiral, biserial or trochoid initial part the number of chambers in the terminal part often decreases. In these cases the shell becomes quadriserial, triserial,

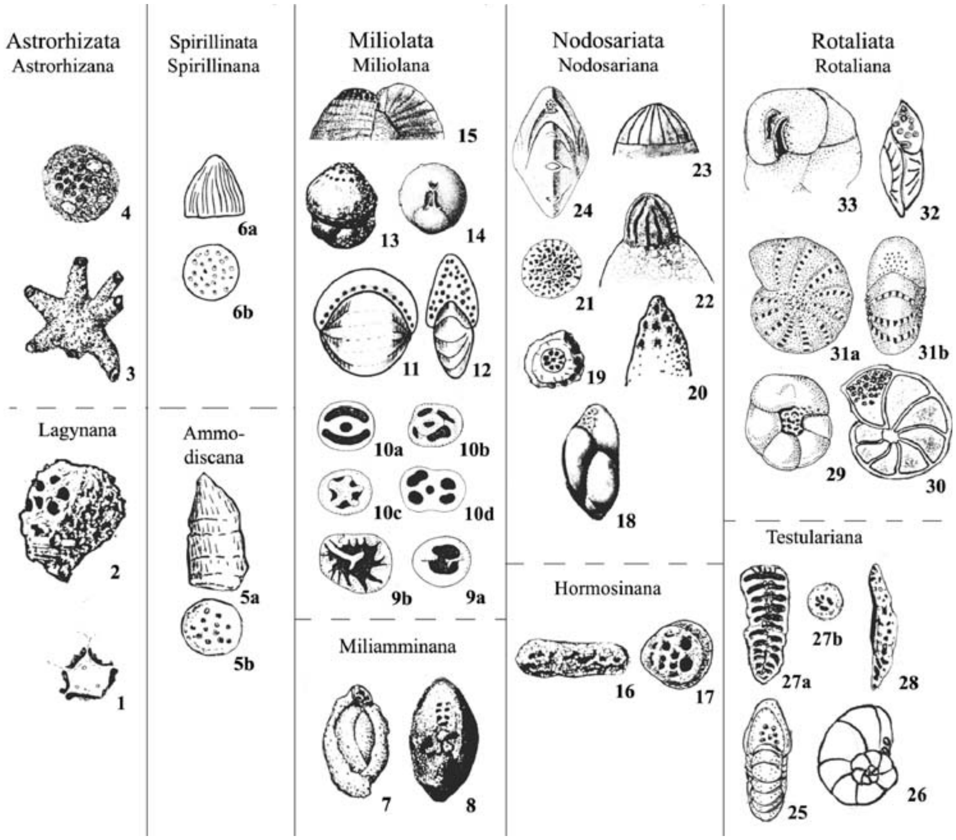

Fig. 6. Polymerization of apertures in different Foraminiferal classes. ***1–4* – class Astrorhizata** (1, 2 – subclass Lagynana, 3, 4 – subclass Astrorhizana), primary polymerized aperture: 1 – *Microcometes*, 2 – *Guanduella*, 3 – *Astrorhiza*, 4 – *Orbulinelloides*; ***5, 6* – class Spirillinata** (5 – subclass Ammodiscana, 6 – subclass Spirillinana): 5a,b – *Haurania*, 6a,b – *Ferayina*; ***7–15* – class Miliolata** (7, 8 – subclass Miliamminana, 9–15 – subclass Miliolana): 7 – *Ammomassilina*, 8 – *Lituola*, 9a, b – polymerization of the inner teeth in *Dentostomina*, 10a–d – multiple aperture of Miliolids as a result of teeth fusion, 11 – *Ovalveolina*, 12 – *Pseudedomia*, 13 – *Rhapydionina*, 14 – *Pyrgoella*, 15 – *Pseudohauerina*; ***16–23* – class Nodosariata** (16, 17 – subclass Hormosinana, 18 – 23 – subclass Nodosariana): 16 – *Polychasmia*, 17 – *Cribratina*, 18 – Delosina, 19 – *Amphimorphina*, 20 – *Cribropleurostomella*, 21 – *Cribrolenticulina*, 22 – *Laevidentalina*, 23 – *Pandaglandulina*, 24 – *Cribrorobulina*; ***25–33* – class Rotaliata** (25–28 – subclass Textulariana, 29 – 33 – subclass Rotaliana): 25 – *Cyclammina*, 26 – *Entzia*, 27a,b – *Cribrogoesella*, a – section, b – apertural view, 28 – *Poritextularia*, 29 – *Sestronophora*, 30 – *Anomalinella*, 31a, b – *Elphidium*, 32 – *Cribroparrella*, 33 – *Anticleina* (Cassidulinidae)

biserial or uniserial at the end. In some species all the successive changes are visible, reflecting the process that has taken place over geologic time. Oligomerization taking place step by step sometimes is not complete, for instance the flabelliform shell of some initially planispiral shells may or may not be transformed into an annular one (Fig. 5: *8*) when only the one chamber forms the whole whorl instead of the several chambers per whorl in the initial planispiral part. The process of oligomerization leads as a rule to the enlargement of the oligomerized structures in their size and to the intensification of their functions. Thus the dimensions of the last chambers which became few or single in number exceed the dimensions of the more multiple chambers of the previous volutions by several times (Fig. 5: *2, 3, 8d, 12, 17, 18, 22–26*). The processes of oligomerization of the chambers take place in parallel in all the phyletic lines of the multichambered representatives (classes Spirillinata, Miliolata, Nodosariata, Rotaliata) in their calcareous representatives, and often in the agglutinated forms as well. Thus even in the Spirillinata where cases of chamber oligomerization are comparatively rare (in connection with the weakly developed multichamberedness) such examples can be found: in *Patellina* after a short distance of the tubular chamber following the proloculus the 1–2 whorls containing up to 5 chambers per whorl, then – 3, and very soon – only 2, forming the major part of the shell. The oligomerization of the chambers per whorl from the initial 6 to the terminal 3 is also evident in *Paleopatelinella*, from 5 or 3 to 2 – in *Patelinella* (Fig. 5: *2, 3*). Some other examples of oligomerized chambers in the classes Miliolata, Nodosariata and Rotaliata (where such examples are more) are given in Fig. 5.

The highest degree of the chamber oligomerization is achieved in the classes Miliolata (*Idalina*), Nodosariata (*Colaniella*) and Rotaliata (Globigerinana – *Orbulina*) when the single last chamber embraces the whole shell (Fig. 5: *10, 18*).

As mentioned above, the oligomerized chambers are usually of greater dimensions than the preceding ones. In all these cases the lesser amount of structures (chambers) fulfills the functions of the more numerous ones and hence the intensification of functions also exists.

Polymerization and oligomerization of apertural structures in the foraminifera

Among other shell structures, the functionally important aperture and its structural elements can also be polymerized (or oligomerized). This polymerization also goes in parallel in the different phylogenetic lineages. Thus the polymerization of the apertural openings on the apertural face can be observed in the agglutinated and calcareous Nodosariata (Fig. 6: *16–24*) (*Polychasmia, Cribratina* – Hormosinana, in *Laevidentalina*, *Amphimorphina*, *Cribrolenticulina*, *Hemirobulina*, *Vaginulinopsis*, *Saracenella*, *Delosina* – Nodosariana), Rotaliata (Fig. 6: *25–33*) (*Cyclammina*, *Entzia*, *Tawitawia*, *Cribrogenerina*, *Colomita*, *Cribrogoesella* – Textulariana, *Duostomina*, *Candorbulina*, *Acostina*, *Bifarinella*, *Anticleina*, *Rugidia*, *Eponides* and *Poroeponides*, *Hofkarina*, *Neocribrella*, *Sestronophora*, *Cribroelphidium* and *Elphidium,* and some others – Rotaliana) and especially in the Miliolata (Fig. 6: *7–15*). In the last class the numerous agglutinated (*Debarina*, *Trochamminita*, *Mayncina*, *Stomatoecha*, *Kolchidina*, *Lituola*, *Acruliammina*, *Acupeina*, *Bulbophragmium*, *Cyclolina*, *Choffatella*, *Spirocyclina* and others – Miliamminana) and calcareous genera with secondary multiple aperture (*Cribrolinoides, Inaequalina, Hauerina* and other forms with trematophore, *Cribropyrgo*, *Nevillina*, *Crenatella*, *Poroarticulina*, *Pyrgoella*, *Fabularia*, and others – Miliolana) is even difficult to enumerate. In Spirillinata such examples can be noted in the higher Spirillinana (in *Angotia*, *Chapmanina*, *Ferraina* – Fig. 6: *6*), in the agglutinated forms in *Haurania* (Fig. 6: *5*) and related genera questionably referred to this class (Mikhalevich, 2004). They are not numerous in this group.

The inner structural apertural elements such as Miliolata teeth (when there are two or more in one aperture) and Nodosariata radial ribs also represent polymerized structures (Fig. 6: *9*). The coalescence of the separate elements of the aperture into a united structure shows the process of oligomerization of these units (Fig. 6: *10, 19, 22*) going in parallel in the different genera of both classes. In these cases, the oligomerization of the elements of the inner apertural structers results in the polymerization of apertural openings thus demonstrating the interconnection of both processes. In the Rotaliata where the inner apertural elements (different tooth-plates and so on) are extremely strongly developed, their polymerization within the single aperture does not take place in the strict sense (though the different parts of the complex tooth-plate in the buliminids for example could be regarded to some extent as polymerized and at the same time differentiated).

But the formation in the higher Rotaliata (Buliminida, Bolivinida) of the integrative apertural systems (Mikhalevich & Debeney, 2001) extending from chamber to chamber exemplifies the appearance of apertural and organismic systems on a more advanced, new level of organization. Thus polymerization of the structures of the apertural system in this case also takes place.

The multiple apertural openings in the unilocular tectinous or agglutinated Astrorhizata (*Microcometes*, *Guanduella* – Lagynana, *Orbulinelloides*, *Astrorhiza*, and others – Astrorhizana) and Lagenids (*Cribrolagena* – Nodosariata) are regarded here as primary multiple (see Mikhalevich, 1995). The circular or more often irregular openings without definite position obviously arose primarily. The next step in the development of such forms results in the appearance of a single aperture of definite position and usually of larger dimension (*Apogromia*, *Paralieberkuehnia*, *Psammophaga*, *Saccammina*, *Lagena*). Their apertures can be regarded as oligomerized and secondarily single. The strict localization often takes place during the process of oligomerization.

The appearance of additional (secondary, supplementary) apertures (sutural, umbilical, peripheral ones) also represents the polymerization of the apertures and at the same time the rise of the new apertural structure on a new level. Additional apertures are mostly and widely developed in the agglutinated (*Norvanganina*, *Plotnikovina*, *Polystomammina*, *Rotaliammina*, *Toretammina*, *Trematophragmoides*, *Balticammina*) and especially in the calcareous Rotaliata (*Schwantzia*, *Pseudoeponides*, *Strebloides*, *Trochulina*, *Epistomaria*, *Cribroelphidium*, *Globigerinoides*, *Pseudobuliminella*, *Virgulinella*, and others). They arose in parallel in the calcareous representatives of the class Spirillinata (*Trocholinopsis*, *Hergotella*, *Lasiodiscus*, *Howchinia*). They are not developed in the classes Miliolata and Nodosariata where they appear only as an exception (*Polysegmentina* – class Miliolata, *Delosina* – class Nodosariata).

In all cases of polymerization and oligomerization of the apertural structures discussed above the evolutionary changes have led to the intensification of the functions of the aperture where the cytoplasmic flows are most intense and need more space and support.

Polymerizational/oligomerizational processes in the plane of symmetry of the foraminiferal shell

The number of the axes and of planes of symmetry also is a subject of the processes of polymerization and oligomerization. Sphaerical forms have multiple and equal axes, the appearance of planispiral and trochospiral forms with a smaller number of unequal axes could be considered as a progressive one. Sometimes a sphaerical form could be of secondary origin (*Orbulina*) thus repeating the initial form at a new level of organization. The elongated forms with longitudinal axes could also be of primary (*Rhabdammina*, *Hyperammina*, *Hormosinella*, *Syzrania*, *Nodosaria*) and secondary (*Dimorphina*, *Clavulina*, *Rectobolivina*, *Siphogenerina*, *Pseudobuliminella*) origin (in this last case originating from the planispiral and trochospiral forms).

DISCUSSION

In the Foraminifera, as well as in other Protista, the processes of the polymerization play an exceptionally large role compared with the Metazoa. This is connected with the small sizes of the unicellular organisms and the importance for them to enlarge their dimensions and a number of structures. For them it is nearly the only method of activation and intensification of their functions and their high plasticity. Poljanskiy & Rajkov (1977) explained the predominance of the processes of polymerization in Protista with a low level of organization of their elements, which is close to the molecular level and the distinguishable features of molecular constructions are their stability and rigidity. According to these authors this fact nearly excludes the possibility of the complication of the inner structure of the organism of the unicellular level and makes the method of the intensification of functions by the processes of polymerization the most available for them. Larin (1977) showed that the cell itself, its organization, its nuclear and cell membranes, all its organelles are the result of the biopolymerization of the vesicles and of other elemental structures. He considers the hypothetical organelle of the first order to be “the biomer” consisting of nucleoproteids.

Polymerization is the primary process foregoing the process of the oligomerization. The latter process can take place when there are already preformed structures consisting of numeral elemental units. This process usually takes place in the more advanced forms. The processes of the polymerization and oligomerization are interconnected, are often complex and multiphase (for example the multiphase multichamberedness). As stated in the previous chapter, such processes lead to the differentiation and integration of the organism structures, promote the transition to the next level of organization (the supermultichamberedness causes the appearance of integrative systems (stolons, tunnels and canals), the polymerized nuclear apparatus leads to the separation of nuclear functions and the nuclear duality).

It is interesting to note that the polymerized nuclei (along with the nuclear duality) and polyploidy are more widely known among the higher representatives of the Miliolata and Rotaliata having a complex calcareous shell. The analysis of the available data permits us to elucidate the tendency of the development of the nuclear apparatus from the more primitive to the more advanced forms. All this indicates a long and complex developmental pathway of the foraminifera and their singularity among other protistan groups. Comparing the nuclear foraminiferal apparatus with that of the former Sarcodina such as Radiolaria (one highly polyploid nucleus) and Acantharia (multinuclear, obviously without polyploidy) it turns out that foraminifera used in their evolution not one, but both of the possible pathways of polymerization of the nuclear apparatus. Infusoria also passed both these ways and above it – the process of the oligomerization of the nuclei. The fate of the foraminiferal macronuclei during the process of reproduction (they degenerate and are not inherited by the daughter individuals) and their life cycles also differ from these of the Infusoria. Infusoria had been long considered to be a separate phylum. The taxonomic conclusion resulting from the analysis performed supports the separation of the foraminifera also as a phylum.

The nuclear dimorphism in foraminifera, the profound differentiation and the separation of functions inside the nuclear apparatus could be considered as aromorphosis (complex achievements promoting the significant progressive evolutionary changes). The emergence of multichamberedness can also be considered in the same way. The multichamberedness of the foraminifera could be regarded in an evolutionary view as the analogue of multicellularness when the elevation of the complexity and the energy of the organism is going at the unicellular level on the account of the polymerization of the intracellular components rather than the polymerization of the cells. This is the unique evolutionary pathway of the foraminifera which does not occur in any other animal group.

As was shown above, the processes of polymerization and oligomerization take place independently and in parallel in different phyletic lines (classes), for instance the multiplication of the nuclei (practically in all the lines, though less expressed in the class Astrorhizata, – in the class Nodosariata unstudied yet), the nuclear duality (in the higher representatives of the classes Miliolata and Rotaliata) (Fig. 3), true multichamberedness (Fig. 4, and Mikhalevich, 1981, 2000; in the higher representatives of the classes Spirillinata, Miliolata, Nodosariata, in all the representatives of the class Rotaliata), supermultichamberedness and the origin in this connection of a new organismic integrative systems (stolons, tunnels, canals) of the Miliolata and Rotaliata (in the case of the Spirillinata the primitive canal system arose in pseudotwochambered shells with multiple volutions of the undivided tubular chamber). The oligomerization of the chambers in the last volutions also took place in several lines (Fig. 5). The polymerization of the apertural openings is especially widely distributed (Fig. 6). The tendencies of the basic evolutionary changes of cytological and nuclear structures and of progressive changes in the skeletal structures evolve in foraminiferal groups in parallel and their directions coincide to a significant extent.

The rates of the processes of polymerization and oligomerization vary in different groups, the investigation of the tempo of these rates could also help in the construction of a proper classification.

The geological successions and the geological record give us the possibility to evaluate the advancement of the evolutionary process in particular lineages. According to the multiple or to the oligomerized state of the structures it is possible to establish the degree of primitiveness of the group or the comparative remoteness of their origin. Thus the investigation of these processes helps to solve some phylogenetic problems, to judge the direction of phylogenetic development (e.g. the oligomerization of the number of chambers in the initially planispiral or trochospiral shells when the uniserial or circular terminal parts are developed – Fig. 5, the degree of the differentiation of the nuclear apparatus). Grell (1979) underlined the specificity of the homokaryotic spirillinids (with patellinids), their distinction from the heterokaryotic rotaliids and the inadmissibility of uniting both into one taxon as sister groups.

The results of the study of polymerization and oligomerization processes are very important for taxonomic studies permitting the construction of the taxonomic systems based on the evolutionary significant features.

CONCLUSIONS

The rules of the evolutionary development realized through polymerization/oligomerization processes were studied previously mostly at a multicellular level in the Metazoa. Here I have attempted to determine whether these rules and regularities could be applicable at the unicellular level. The analysis of the morphologic development of some Protistan groups, mainly the foraminifera, had shown that the basic rules of evolutionary development such as Dogiel's (1929, 1954) concept on polymerization and oligomerization of the structures of the organism, leading to the further differentiation and integration of these structures in their morphology and functions could be seen in the foraminifera as well. Concerning their usually minute dimensions the processes of polymerization are more developed at this level of organization giving the primary base and new opportunities for following the processes of the oligomerization and differentiation. The predominance of the processes of polymerization characterizes the qualitative specificity of the evolution at the unicellular level of organization.

In the foraminifera among the main polymerised structures are the number of nuclei and the genomes inside the nuclei (polyploidy), the number of chambers, the number of apertural openings and of the elements of the inner apertural structures. The polymerized foraminiferal nuclei did not pass through the process of oligomerization, as opposed to the representatives of the phylum Infusoria. The polymerized elements of the foraminiferal skeleton are undergoing the process of oligomerization as well. At the base of the preceding polymerization and oligomerization new organismic differentiated and integrative structures emerge: the embryonal specialized chambers, such integrative structures as stolons, tunnels and canals, integrative apertural systems. These structures represent a new level of polymerization, the multiplication of the organism systems, of the structural levels in one cell. The increasing of the number of structural levels in the organism is the basic process of progressive evolution. Thus these processes promote the mechanism of transition to a new level of organization, thereby gaining universal significance. The complexity and the multiphase character of the processes of polymerization and oligomerization facilitates and provides the processes of differentiation and integration, opens the ways to the further evolutionary changes which gives the organism a higher degree of its wholeness, and the activation and immobilization of its functions. The processes of polymerization and oligomerization as the major pathways of the macroevolution are applicable to the foraminifera. In their different groups they progress independently and in parallel. The study of these processes aids in the understanding of the evolutionary development of the group and in the composition of its natural classification.

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