



The Current State of Foraminiferal Research and Future Goals

Valeria I Mikhalevich*

Zoological Institute of the Russian Academy of Sciences, Russia

***Corresponding author:** Valeria I Mikhalevich, Zoological Institute of the Russian Academy of Sciences, Universitetskaya Nab., 1, 199034 St. Petersburg, Russia, Email: vm38600@gmail.com

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Abstract

An overview is presented of the main achievements in studies of the phylum Foraminifera during the previous few decades, especially the last half of the 20th and the beginning of the 21st centuries, and of the most urgent goals of future studies with a special attention to the problems of classification as a base for all other studies.

Keywords: Foraminifera; Morphology; Ecology; Zoogeography; Biology; Molecular Studies; Systematics; Previous Achievements; Goals of Future Research

Overview of the Most Important Achievements in Different Fields of Foraminiferal Research

Foraminiferology dates back to 1826, the year of d'Orbigny's publication on this group of organisms. More than 5000 genera and more than 40,000 fossil and 10,000 recent species have been described so far. The fundamental role of Foraminifera as sensitive indicators of modern and ancient environments is widely known and they are used in ecological studies including pollution monitoring, as well as in petroleum exploration, for applications in biostratigraphy, paleoecology and paleoclimatology, and in many other fields of research.

At the end of the 20th and beginning of the 21st centuries, significant progress in all these foraminiferal studies has been achieved. In addition to traditional research marine areas, Foraminifera were discovered in hypersaline waters as well as in brackish and even in fresh waters [1-4], as well as in ground waters of special high salinity composition [5-7], primitive foraminiferal forms were discovered in soil communities [8]. Extremely important evidence of the role of benthic foraminifera in the process of denitrification of

sediments was experimentally obtained [9,10].

A number of works have been devoted to foraminiferal feeding, their role in the food-chains [11-15], to the other aspects of their biology [16-19], to their symbionts [20-30], to the process of growth and formation of the new chambers [17,31-36]. Even the problems of foraminiferal infestation and diseases and dormancy were touched upon [37-40].

Ecological studies of this period achieved a new level being strictly coordinated with the physical parameters of the studied environments and using new techniques and methods. Laboratory experiments permitted to study the effects on the different foraminiferal species and populations of not only natural, such as t, salinity, O₂ and CO₂ concentrations, pH and trace elements, but also fuel oil and heavy metal pollution (mercury, cadmium, plumbum). These laboratory results received during the last decades can be found in excellent review of Kathal, et al. analyzing and summarizing such studies.

Problems related to ocean acidification [41], even experimentally shown [42], to the oxygenation of bottom waters [43-45], organic carbon flux [46-52] influencing foraminifera were also investigated.

Studies concerning recent foraminiferal distribution cover now all areas of the ocean including the Arctic and Antarctic and inland seas, and although their study is far from being uniform, nevertheless, it seems that there are no more absolutely blank spots left on the map.

In a short review, it is impossible to mention all the significant publications in these fields.

The amount of knowledge accumulated about the paleogeographic distribution of foraminifera, the knowledge in paleoecology, paleoclimatology, in the study of the influence of ancient volcanic activity on their propagation and extinction, data received in stratigraphy - also does not allow to name here even the most important publications. But the results of the great DEEP SEA DRILLING PROJECT, the blue volumes published after the expeditions, the multiple zonal scales and finally the global correlation of geological deposits elaborated cannot be failed to mention [53-55], as well as the painstaking work of revising the geological ranges of many genera [56,57].

The significant volume of the new data on the foraminiferal nuclear apparatus and its changes during the life cycle, nearly unknown previously, was accumulated during these decades [11,17,19,20,58-83]. These results made possible for the first time to use the characters of the nuclear apparatus in the diagnosis of high rank taxa (classes) [83-85]. Even the most important works in this direction cannot be listed in a short review; more complete list can be found in the Mikhalevich [83] book. These new studies affected, to one extent or another, all classes, except for the Nodosariata class. Some new methods of research were introduced, one of the most significant of which that started a new era in the foraminiferalogy were the first applications of electron microscopy to studies of not only skeletal (as it was before since the beginning of the EM studies of the shell wall), but also cytoplasmic structures, cytophotometry of the nuclei in the process of reproduction [64,86].

Since the middle of the 20th century traditional attention to the foraminiferal shell wall as to one of the highly important systematic characters received new opportunities with the Scanning Electronic Microscopy (SEM). It caused the real explosion of the studies of the shell wall ultrastructure nearly in all of foraminiferal classes, both for agglutinated and calcareous variants of shell wall. These studies are widely known and so numerous that it is impossible to site even the most known among them (the list of publications could be found in [83]). Unfortunately, the representatives of the class Nodosariata were unlucky in such investigations. A few results were not able to show the real picture of their calcareous shell wall, obviously because their thinnest structures needed significantly higher magnification. The principally specific

organization of the Nodosariata calcareous shell wall was clearly demonstrated with the more perfect Zeiss Sigma VP field emission scanning electron microscope (FESEM) by the Polish authors [87] thus adding one more character to the class diagnosis. Some similar pictures of the Nodosariata's calcareous shell wall were received somewhat earlier [88] (Figure 1), but the quality of the photos received with the less advanced SEM model (Hitachi SEM, model S-570) was of the less clear quality.

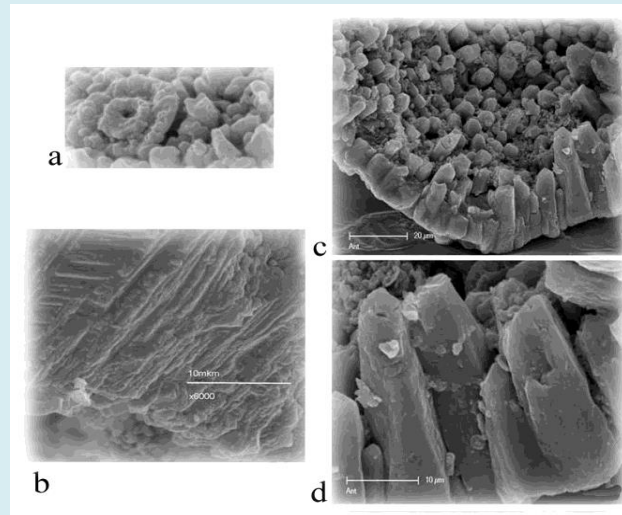


Figure 1: Shell wall ultrastructure of the two *Strictocostella* shells [88].

- Rough outer surface and pore openings of *Strictocostella matanzana* (Palmer and Bermudez) 1936, with a pore opening between and inside the tubercles (enlarged view of the chamber wall, (x5000).
- Part of the transverse breaking of the chamber wall of *Strictocostella matanzana* (Palmer and Bermudez) 1936, showing partly inclined parallel plates going from the inner part of the chamber up to the surface and pierced by the narrow pore openings going in the same direction (x 6000).
- Part of the broken last chamber of *Strictocostella matanzana* (Palmer and Bermudez) 1936 *perytæ* Mikhalevich, [88] showing the polygonal crystals (x 3000).
- Strictocostella matanzana* (Palmer and Bermudez) 1936 *perytæ* Mikhalevich, [88] – part of the previous photo c - showing enlarged polygonal crystals at the edge of the transverse breakage of the chamber wall with the pore opening inside the broken polygonal crystals (x 6000).

The other important event of the last decades of the 20th century was the use of molecular genetic methods – the event of the highest importance in biology. In the

study of foraminifera these principally new molecular methods permitted to identify several main phyletic lines (clades) (see below) [89-93], as well as to document some minor clades of marine and even fresh-water foraminifera [94,95], to define the position of Foraminifera among the other unicellular Eukaryotes [96,97], to interpret geological age of the main clades using molecular clock analysis [98]. Molecular studies have revealed a twice greater diversity of phylotypes than morphotypes in some single-chambered (monothalamous) foraminifera [99-103], and high genetic variability of some planktonic species [104-108]. They also documented the possibility of existence of a pelagic stage in the life cycle of benthic species [109], and gave many other important, sometimes unexpected results. These methods gave new insight into foraminiferal zoogeography and phylogeography [110-114], molecular ecology using sequencing of environmental DNA (eDNA metabarcoding) gave the possibility to receive necessary results thousands of times more effectively than was possible with traditional methods [115,116]. Metagenomic sequencing became a common, powerful approach to study diversity and functional relationships in marine ecosystems.

Overview of the Most Important Achievements in Foraminiferal Taxonomy and Its Current State

The basis for analysis of all the observed and studied facts and phenomena are classification systems. The word "taxonomy" itself speaks of a systematic approach, which is the most important and generalizing knowledge, the highest level of scientific research, helping to understand the relationship of the studied objects, and the patterns of their development. The most important, outstanding event in this area of Foraminiferology was the publication of a monumental two-volumed edition by Loeblich and Tappan [117], which included all genera and suprageneric taxa known by that time with their complete diagnoses and synonymy. It has become a reference book for every specialist – foraminiferologist. This morphological classification strictly following nomenclatural rules served and still serves as a firm base of classification stability. Its role and importance, its contribution in the development and achievements of all the fields of foraminiferology can hardly be overestimated, it became and remains still an indispensable tool for identification of foraminifera.

From the time of the first foraminiferal classification systems to the most recent, the number of their families has increased from 5 or 10 [118,119] up to 499 [83,85] and is constantly increasing. Historically, two main themes in the higher systematics of the foraminifera have existed, which could be roughly outlined as follows: (1) Those giving the predominant significance to the shell wall

composition, and (2) giving the predominant significance to the plan of structure of the organism reflected in their shell morphology. The electron microscopy that documented shell ultrastructural elements and their diversity strongly stimulated the 1st of them. The same approach was adopted in the Loeblich and Tappan [117] classification.

The 2nd approach predominated in the Russian foraminiferological school. It began with Rauser-Chernousova and Fursenko [120] and resulted in the creation of a new foraminiferal macrosystem based on fundamentally new concepts of their evolution and classification which was elaborated after thorough analysis of morphological and ultrastructural data of representatives of not only Recent but of all the geological periods since the Cambrian [83,85,121-125]. According to these views, foraminifera were regarded as a phylum embracing 5 classes: Astrorhizata Saidova, 1981, Miliolata Saidova, 1981, Spirillinata Mikhalevich, 1992, Nodosariata Mikhalevich, 1992 and Rotaliata, Mikhalevich, [121] (Figure 2). It was shown, that each of these classes represents the separate phylogenetic line that arose independently and in parallel during geological history and achieved in their development a different degree of complexity [84,122]. The agglutinated shell wall, and then the more perfect secreted calcareous wall also arose in parallel in different classes [84] elaborating a special mode of ultrastructure in the calcareous representatives (subclasses) of each of the lines (classes). Morphological analysis permitted to unite the agglutinated trochamminids with discorbids and other rotaliids, some ammodiscids with spirillinids, some agglutinated representatives included earlier into different taxonomic groups – with nodosariatas [121,122,123], miliamminids with miliolids [125]. The formerly heterogenous (polyphyletic) Textulariina, which previously united all the possible foraminiferal morphotypes into a single taxonomic group, were split into several groups according to their morphology and placed as a more primitive subclasses with an agglutinated shell wall as the base of the other multichambered classes [84,121,123] (Figure 2). The more advanced calcareous subclasses of each phyletic line have a calcareous ultrastructure peculiar to each of them, thus the test ultrastructure also has an important albeit subordinate taxonomic significance in comparison with the shell morphology, and it is characteristic for not class-level but subclass-level taxonomy. Under this approach, the agglutinated and calcareous forms of similar morphology within each phyletic line regarded as related [84,121,125], and this is contrary to previous views regarding their similarity as result of convergence. The classification of Kaminski [126-128] embracing agglutinated forms combines to some extent both approaches making it easier for non-taxonomic researchers to identify the taxonomic position of their material.

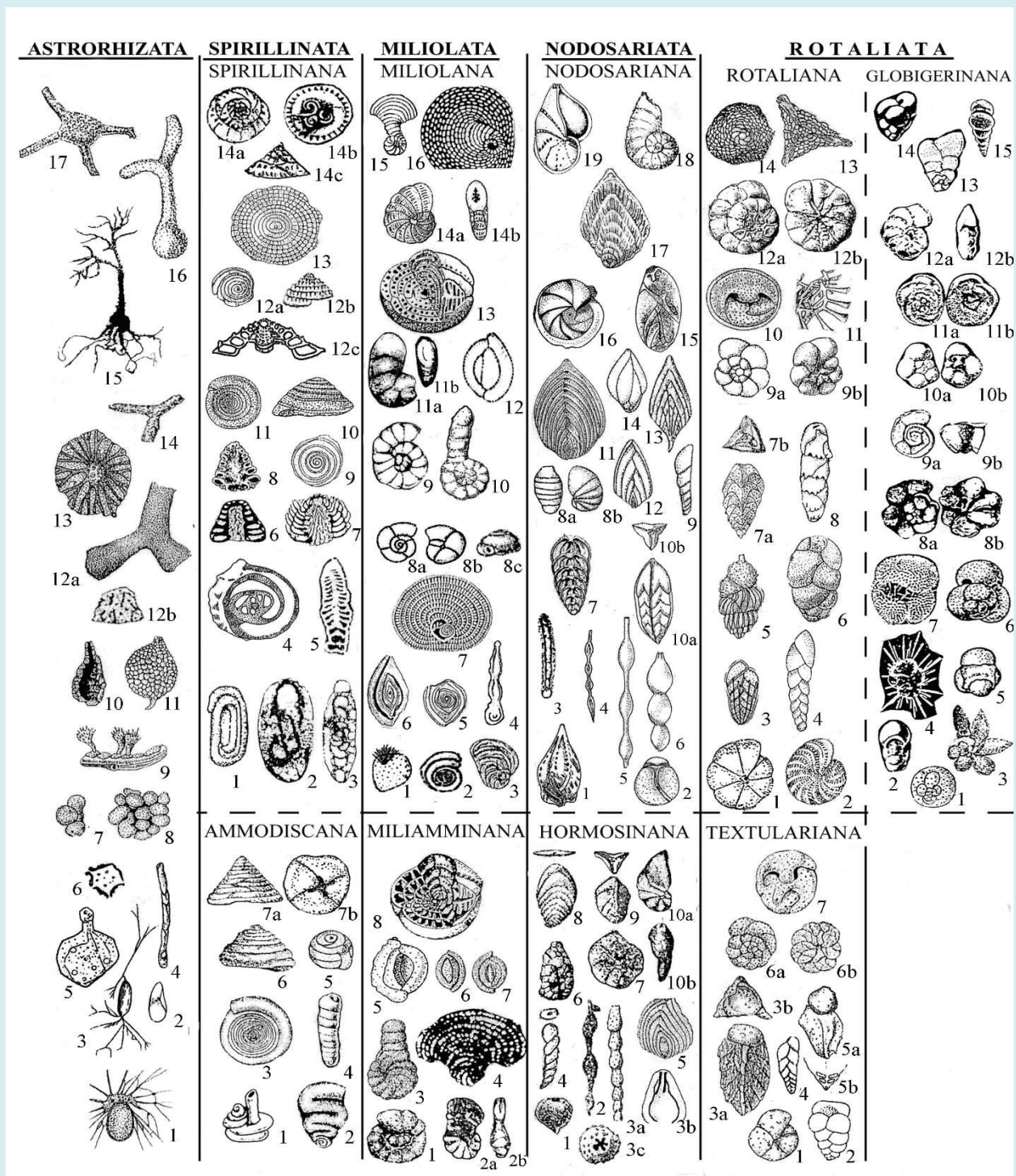


Figure 2: Morphological classification of the Phylum Foraminifera [83,84,85,121-125]: borders between classes marked by complete line, borders between subclasses – by the dotted line (after Mikhalevich, 1992 – modified).

Molecular methods furnish an opportunity for new insight into foraminiferal taxonomy providing taxonomic criteria independent of morphological characters. They

already confirmed the monophyly of the foraminifera within the other unilocular Eukaryotes supporting its phylum rank, and within the foraminiferal phylum 4 major clades were

revealed [92]:

1. Unilocular agglutinated and soft-walled shells called as the new class Monothalamea and fully corresponding in their composition and diagnoses to the previous morphoclass Astrorhizata Saidova.
2. The multilocular class Tubothalamea uniting two clades corresponding to the morphoclasses Miliolata Saidova, 1981 and Spirillinata Mikhalevich, 1992, which fundamentally differ from each other based on their shell morphology and shell-wall ultrastructure, moreover, their nuclear apparatus are fundamentally different (see diagnosis of the classes in Mikhalevich, 1992, Mikhalevich et Debenay, 2001) [83,84,85,].
3. Multilocular class Globothalamea corresponding to the full morphoclass Rotaliata Mikhalevich, [121] though it also includes a minor clade containing a few representatives surely belonging to the morphoclass Nodosariata according their shell structure and shell wall ultrastructure. In Globothalamea there is also a small clade including *Glandulina* and *Lenticulina* species which surely belong to the Nodosariata morphoclass according to their shell structure and shell wall ultrastructure. *Glandulina antarctica* of this minor clade also differs from that of Rotaliata (= Globothalamea) class in its sequence [92]. These are the only discrepancies concerning these three classes between the two classifications, which may be due to the lack of living studied material as well as difficulties with the molecular study of the hard-shelled foraminifera or because of some other reasons. Thus Nodosariats are again unlucky not being touched by the necessary studies.

The morphoclass Nodosariata was only slightly touched with the studies at the molecular level (a small clade in Globothalamea, such investigations were later began [92] when it was considered that the sequence of *Glandulina antarctica* also differs from that of the Rotaliata (= Globothalamea) class [92]. Each of the molecularly revealed clades of the multichambered forms includes agglutinated and calcareous forms of similar morphology just as was stated in the new morphological classification devised in the Russian School studies between 1980 and 2013 mentioned above. Morphological characters having the primary significance in the diagnoses of each of the molecular classes are the same as in the new morphological classification of the Russian School (1959, 1980–2013) as opposed to the previous traditional classifications: these are plan of structure including shell and chamber form, the prevailing mode of coiling, position of the aperture and its structure (later more often named as distance between successive apertures, though in some cases it does not coincide), etc – in distinction to the prevalent significance of the characters of shell wall composition and ultrastructure in the preceding widely accepted classifications when, for example, forms representing principally all the known varieties of foraminiferal shell

structures and the only common feature - their agglutinated shell wall, were united in one taxon Textulariina. Thus, the separation of the Astrorhizata class (= Monothalamea) and multichambered morphoclasses Miliolata (Tubothalamea) and Rotaliata (= Globothalamea) as well as uniting of the agglutinated and calcareous forms within each phyletic line (class) according their morphological features were also confirmed by molecular studies (though less elaborated in molecular studies Spirillinata clade was united in molecular classification with the Miliolata clade). The confirmation of the monophyletic character of the phylum foraminifera and of three of its classes separated previously on the basis of morphology is a great achievement of the new molecular methods and its significance may be compared with the NASA Gravity-Probe program which confirmed Einstein's theory of relativity. At the same time it also confirms the significance of morphological studies and their usefulness for reconstructing of the true evolutionary phyletic lines.

As it was mentioned above, the fourth less studied by molecular methods morphoclass Spirillinata though showing its line, was united with the morphoclass Miliolata. Unfortunately, the 5th morphoclass Nodosariata was nearly overlooked in the molecular studies and it still needs the greater attention, all its multiple taxa were placed in molecular classification scheme as Incertae Sedis. Surely, in all its morphological and shell wall features, in tendencies of its evolutionary development it represents a separate phylogenetic foraminiferal line (class), and on this basis, one can expect that its representatives are genetically different from the representatives of the other foraminiferal classes. A few species examined with such molecular studies (for example *Glandulina antarctica*) already turned out to confirm this assumption being different from the class Rotaliata (Globothalamea) and from the other multichambered foraminiferal class-rank taxa [92].

Thus, Nodosariata again turned out to be investigated less than the other foraminiferal classes. At the same time, this example demonstrates significance of taxonomy helping to elucidate the less studied objects and problems. For instance, for understanding main peculiarities of the life cycles, nuclear apparatus, shell wall ultrastructure, DNA sequences of the main foraminiferal phyletic lines (classes) and Foraminifera as a whole, the study of all these characters in the class Nodosariata would be more important than the additional studies of other not yet studied multiple orders (or of the 11 of the orders in Loeblich and Tappan [117] classification) belonging to the classes where some main features of these characters are known, at least to some extent.

At the same time this example again demonstrates not only importance of morphological methods of study

permitting to understand the main phyletic foraminiferal lines (classes) but also the opportunity to see the most problematic taxa in need of clarification of their systematic position with the help of molecular methods: such taxa, first of all, include some closely related species and genera or primitive shells poor in morphological features, for example, unilocular shells or primitive tubular shells such as *Ammodiscus* whose agglutinated representatives may possibly belong to Miliolata or Spirillinata line being undistinguishable morphologically. Molecular methods can also help in solving such a fundamental problem as the problem of species in Foraminifera, of the species borders which was already brightly demonstrated in some works [104,105,109,129-131]. Morphological methods remain the main, and for the fossil forms - the only ones, methods of study. Thanks to electron microscopy, the resolution and significance of these methods have only increased.

Taxonomy, being the basis for the other disciplines, needs to have stability. Its stability is provided by nomenclature codes with the uniform rules for both Recent and fossil organisms.

The purpose of the code is to ensure that each taxon group has only one correct name accepted all over the world.

"When in the 18th century there was a rapid accumulation of new knowledge, many synonyms and homonyms arose, the situation became close to chaos. This necessitated the creation of nomenclature codes with clear rules while maintaining the principle of priority for all names of the previous period. Thus, the scope of the first zoological code [132,133] included all names published since 1758.

The Main Article of this code first formulated the principle of priority, according to which the correct formal scientific name for an animal taxon, a valid name, correct to use, is the oldest available name applicable to it. This is the most important principle - the fundamental guiding precept that keeps the zoological nomenclature stable. [.....] This made it possible to ensure the universality, stability and continuity of names that have developed over a long previous period, to settle the changing practice in taxonomy." (https://en.wikipedia.org/wiki/Hugh_Edwin_Strickland)

The first codes legalized the already established practice of preserving the very first name, since only such practice could lead out of the maze.

In the 18th - 20th centuries, there was an intensive accumulation of knowledge about organisms described as taxa of a lower rank - from species to family. Therefore, it were the rules for taxa of this lower level that were regulated

in the first codes. Thus these rules did not touch and did not concern taxa of the superfamily rank. Nevertheless, in their practice, scientists adhered to this principle (principle of priority) when describing orders and classes.

At the end of the 20th, the beginning of the 21st century, thanks to the emergence of new research methods, an array of knowledge was accumulated concerning taxa of a higher level - not only of the superfamily rank (which already had been happening for a long time earlier), but also for the those of order and supraorder level, and the class and supra class level also; moreover, names of taxa of the new higher levels appeared, which were not in use earlier (domain and some others). At the same time, the priority of preserving the former taxon's name was often violated, the previous names were not indicated even in synonymy, despite the complete coincidence of the composition and characteristics of the described taxon. This affected all groups of organisms, and to some extent - foraminifera. Among the author names higher than family rank only the order's names authorship survived, but in some cases the rule was violated even in the cases of family level taxa. Under such an approach even the Foraminifera class itself described by d'Orbigny in 1826 (though firstly attributed to mollusks) and several times preserving its author's name even in spite of changing of its rank (from class to the order and then to subclass, again to class and finally to phylum level) would not finally have retained its authorship.

If in the 20th century, in the process of publishing new high rank taxa (order and higher), these fundamental principles of the code were observed in practice, then in the 21st century they often began to be increasingly neglected.

The situation when the names of many groups of organisms began to be used without following the rules of the code (and without mentioning the previous names, even as synonyms) is dangerous and can lead to destabilization of the system similar as it was in the 18th century. The time has come to expand the rules of the code and apply them also to all taxa of a rank higher than the family rank for all groups of organisms. The leading scientists and taxonomists insist on strict adherence to the basic rules of the code when revising new taxa of high rank (class and higher): "Underlying these discussions are principles of nomenclatural priority in the spirit of the codes of nomenclature... As we argued before [134] this [the author meant revision of the taxa - V. Mikhalevich] must be done with care, respecting nomenclatural priority" Adl, et al. [135]. It is very important that this intention is consistently carried out in practice. Thus, for instance, the morphoclass *Acantharea* Haeckel, 1881 preserved its previous name in molecular classification as its composition and diagnoses reflected its monophyletic

character composed at the base of morphological features. Foraminiferal morphoclasses in similar situation were less fortunate – each of the three of them have now two different names.

In the present time when the volume of new knowledge is permanently exponentially growing, role of electronic nomenclature databases, which began at the end of the 20th century is significantly increasing, especially of those giving the classification base. Among them are the Ellis and Messina catalogue which was gradually transformed into an electronic form (<http://micropress.org/em/>), also several sites devoted to traditional and newly offered foraminiferal classifications have appeared:

<http://www.marinespecies.org/foraminifera/> - scientific team headed by B. Hayward (WoRMS) and trying to combine both morphologic and molecular approaches, embracing now more than 18 000 species; S. Brands site <http://taxonomicon.taxonomy.nl/>; <http://www.foraminifera.eu/morphoclass.html> representing suprageneric classification of living organisms, including foraminifera; M. Hesemann site based on the morphologic taxonomy, including already more than 15 thousands of recent and fossil species, and a site devoted to molecular classification including already more than 600 species (the last two sites in the framework of the FEUPRO - <http://www.foraminifera.eu>). S. Brands and M. Hesemann sites use morphologic classifications based on the taxonomic approach elaborated by the Russian school, more details may be found in Mikhalevich [136].

Among the important databases, bibliographic databases also ought to be noted. A list of publications on foraminifera was regularly published by Ruth Todd in the Journal of Foraminiferal Research (<http://www.cushmanfoundation.org/jfr>), more recently also in the journal "Micropaleontology" (<http://www.micropress.org/bim/about.php>). The Grzybowski Foundation (<http://gf.tmsoc.org/foram-refs.html>) covers publications of the main body of micropaleontological journals and monographs from 1980 to the present day. Taking into account the ever-increasing number of journals and publications, it can be said that the Foundation is coping with an almost impossible task. On the same site, great attention is paid to the taxonomy of foraminifera, an International Working Group of Foraminifera Classification (IWGFC) has been created to develop their modern system.

These are, in brief, the main results of the study period under consideration, which can be presented in such a short overview. It can be said without exaggeration that our knowledge of foraminifera in the period under review increased exponentially and surpassed the results of previous centuries.

The Goals and Objectives of Further Research

Taking into consideration the above mentioned, the goals and objectives of further research can be outlined as follows.

1. All previous research directions listed above in Part I deserve to be continued and certainly will be continued using all the possibilities of latest research methods.
2. Studies of living species, their biology, their life cycles, their reaction to different physical and chemical factors in laboratory experiments ought to be significantly intensified as historically the primary attention has been paid to the foraminiferal shells. Nodosariata's representative needs such studies in the first place. It is also worth mentioning the importance of reviews in this and the other topics as, for instance, the review on "Experimental Studies on Benthic Foraminifera" Kurtarkar SR, et al. (2017) and some others. Significance of reviews in a situation of the overwhelming publications number can help to advance the other directions of foraminiferal researches.
3. Cytological methods ought to be more widely used, especially in unilocular forms pure in their shell morphological features. Cytological studies of foraminifera may also contribute to the cell theory and understanding of cell evolution, as foraminifera represent a unique highly specific and advanced group of unicellular eukaryotes.
4. Concerning the fundamental significance of taxonomic studies for all the other fields of foraminiferology it would be important:
 - a. To continue the revision within the major groups (classes, orders) based on new approaches to the foraminiferal taxonomy and evolution offered both by the morphological and molecular schools. Such revision has already been done for the agglutinated groups [123,126-128,137], for miliolates and partially for some other taxa [83,85]. Some representatives of Nodosariata and Spirillinata were transferred from the class Rotaliata to the more appropriate classes earlier – for instance the Paleozoic nodosariates, pleurostomellids [88,122]. Such revision has been started using the molecular methods for the rotaliats [138,139]. But, some of the other major taxa inside the classes ought to be revised using new knowledge and understanding.
 - b. To publish series of articles and monographs devoted to the separate large taxonomic groups similarly as has been done earlier in the Cushman Foundation special publications, in the VNIGRI monographs, in serial of monographs by Hayward [72], Hayward, et al. [140,141], Mikhalevich & Kaminski [137], in thematic issues of *Micropaleontology*, the *Journal of Foraminiferal Research* and some others.

- c. To search and to publish lists of the new genera belonging to different taxonomic groups as well as of the new suprageneric taxa published after the Loeblich and Tappan Treatise of 1987 [117]. The number of genera is steadily increasing, and it is difficult for the specialists who are not purposefully engaged in systematics of the special restricted groups or Foraminiferal taxonomy as a whole to search all the new publications, and sometimes it is impossible not only to navigate the huge number of publications describing new taxa, but also even to track their rapidly growing number. Moreover, it is sometimes difficult to determine the correct position of the new taxon in the foraminiferal phylum. During the last decades such work began and is continued by Kaminski [126,127,142,143,144] for all the agglutinated forms belonging to different foraminiferal classes. I began publications on the new porcellaneous Miliolata genera [136], also tried to add the names of the genera published since 1987 year in systematic review of 2013a book, but for the majority of calcareous forms such special compilation work has not yet been attempted.
 - d. There are problems of high rank taxa nomenclature, especially those of the class and supraclass level not only in foraminifera and the other unicellular Eukaryotes but in all the other groups of organisms including fungi and plants. In fact, now in many of the living groups, there are two parallel nomenclatures for the same objects or the groups of objects, and molecular nomenclature, as opposed to the previous classical one, is not yet regulated by any Nomenclature Codex. At that, it often does not give the synonymy used as the previous names of the new molecular taxa. Luckily, in the foraminifera this problem is not so insurmountable as in the other groups because the 3 molecular classes uniting morphological clades practically coincide with the four of morphological classes and the discrepancies between the morphological and molecular classifications are minimal as compared to the situation with classifications in many of the other groups of organisms. However, the double names for the three of the foraminiferal classes appeared and a number of problems arise due to incompleteness of the groups covered by molecular studies. The prevalence among the foraminifera of fossil taxa also limits the practical use of the new molecular classification not regulated by NCZC.
 - e. All the above mentioned studies and goals (a, b, c, d), especially those marked in the point c,
 - f. Should be regarded as preliminary work for a publication similar to the Loeblich and Tappan "Treatise" of 1987 [117], but based on a new understanding of the system and evolution of the foraminifera and including all the newly published taxa. The need for such an edition is long overdue, and only the united effort and collaboration of specialists can make it possible. Only an edition of this kind may provide "... a firm taxonomic base that serves as a key to the identification of the genera and contributes to the stability of nomenclature." [145]. The absence of such an updated modern complete edition similar to the Loeblich and Tappan "Treatise" of 1987 [117], inhibits and slows down the development of all other directions of foraminiferology.
 - g. To draw attention to the problem of species in the foraminifera and to formulate criteria for their boundaries uniting both morphological and molecular approaches, to study new phyletic lines of multichambered foraminifera with complex morphology discovered by metabarcoding methods in collaboration with morphologists, thus continuing the work began earlier [104,105,129,130,146,147].
 - h. And last, but not the least – to continue to keep strictly following ICZN rules, not ignoring the ethical norms of the code.
5. To continue searching for the roots of the multichambered taxa within the earlier primitive, mostly unilocular forms of the class Astrorhizata (=Monothalamea). These primitive forms are pure in their morphological characters and namely the cytological and molecular methods are perspective in solving this problem. Some of results in this field already received, and new research on the fossil record has uncovered some early examples of multichambered and pseudomultichambered foraminifera in the Ordovician and Silurian [57,148,149-166].
 6. To remember that only an integrated approach using various analytical methods can produce the most effective and promising results.

In conclusion, some ideas that have appeared during my rather long career in foraminiferal studies and which may be of use to younger researchers:

Firstly, in spite of the introduction of new and important methods, the morphological method still preserves its importance: it remains the main method for foraminiferal studies and is practically the only method for fossil forms. Namely, this method permits to formulate the diagnoses of taxa, to perform comparative analysis of different forms, to highlight the taxa with the doubtful taxonomic position, which are in the first place in need of molecular research. Collaboration between specialists in molecular studies with traditional morphologists may bring more fruitful results.

Secondly, the wider a researcher's approach and knowledge of forms and specific problems not only immediate nearest to study but also rather remote, the better may be the results of smaller group studies or immediate problems solved. For example, to understand that fusulinid chomata and recent miliolid teeth are structures identical in their formation and function, one needs to have knowledge of both

groups so widely separated in geological time (Figure 3).

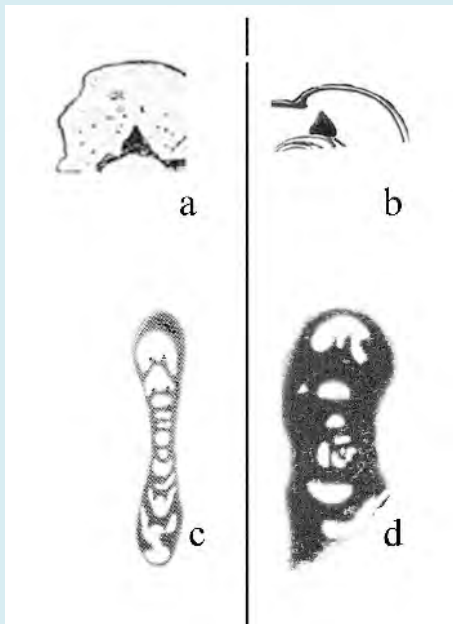


Figure 3: (from Mikhalevich, 2009, part)[124]. Inner apertural structures in fusulinids (a, c) and miliolids (b, d): a – *Endothyra* ex. gr. *similis* Rauser-Chernousova and Reitlinger, 1936; b – *Miliolinella subrotunda* Montagu, 1803; c – *Novella evoluta* Grozdilova and Lebedeva, 1950; d – *Kayseriella decastroi* Sirel, 1999 (after Mikhalevich, 2009 [124]– part) .

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